

H I L G A R D I A

*A Journal of Agricultural Science Published by
the California Agricultural Experiment Station*

VOL. 29

SEPTEMBER, 1959

No. 1

BIONOMICS OF THE RICE LEAF MINER, *HYDRELLIA GRISEOLA* (FALLEN), IN CALIFORNIA (DIPTERA: EPHYDRIDAE)¹

ALBERT A. GRIGARICK²

INTRODUCTION

CALIFORNIA RICE has been notably free of serious insect attacks. In May and June of 1953, however, the larvae of an ephydrid fly, *Hydrellia griseola* (Fallen), were found mining the leaves of rice quite extensively throughout the Sacramento and San Joaquin valleys of California.

The fly was first described in Sweden in 1813. Loew reported it in North America in 1862. It had been considered an economic pest on cereals in Europe and Asia for many years, but was not known to be of economic significance in North America until 1922, when deOng reported its injury to rice in parts of California. No serious leaf miner damage to rice was reported in the literature between 1922 and 1953, although light infestations were noted in 1932 (Cartwright *et al.*, 1933)³ and specimens were sent to the University of California for determination in 1951. Within a period of six weeks in 1953, between 160,000 and 190,000 acres of rice were treated with insecticides. Much of the acreage was treated as an emergency measure, as the full potentialities of this insect were not known. Lange *et al.* (1953) reported the successful control of the insect, and summarized the meager information known of its biology and ecology in California.

The present study was initiated in 1954 to obtain a detailed knowledge of the bionomics of the species. Phases of the three-year study that received special attention included the relationship of the seasonal life history on wild host plants to cultural practices, the climatological conditions which favor initial infestation and continued mining of rice, and the role of natural enemies in maintaining a biological balance of this insect. Laboratory experiments, designed to supplement field observations, emphasized the effects of temperature and humidity upon the species and suggested an explanation for periodic intervals of limited abundance in restricted and localized foci.

¹ Received for publication July 23, 1958.

² Assistant Entomologist in the Experiment Station, Davis.

³ See "Literature Cited" for citations referred to in the text by author and date.

HISTORICAL BACKGROUND

A review of the literature dealing with *Hydrellia griseola* reveals numerous publications, but most of these are merely brief economic listings. The author included in the historical review below, for the most part, only those publications which stress original work, or which contain information of the greatest utility to future workers.

Fallen (1813) originally described the species as *Notiphila griseola*.

Macquart (1835) placed *Notiphila griseola* in the genus *Hydrellia* of Robineau-Desvoidy (1830).

Loew (1860) redescribed *H. griseola* and separated it from related species mainly by color.

Lilljeborg (1861) reported *H. griseola* on barley, oats, and timothy in Sweden, which is the first known reference to it as an economic pest.

Loew (1862) briefly described several species of *Hydrellia* in North America. He included *hypoleuca*, *obscuriceps*, and *scapularis* which were later reduced to varieties of *H. griseola*.

Stein (1867) reported on the biology of *H. griseola* on barley and described and figured the adult and larva.

Jones (1906) published a catalogue of the Ephydridae. It included a literature review, list of known species of *Hydrellia*, and a key to North American species.

Grunberg (1910) discussed the characters of the genus *Hydrellia* and the general habitat of its members, gave a key to the species, and figured the head and thorax of *H. griseola*.

Linnaniemi (1913) reported the host plants, description of damage, and life history of *H. griseola* in Finland.

Malloch (1915) described and figured the larva and puparium of *H. scapularis*, and gave its host plant, habitat, and parasitism in Illinois.

deOng (1922) reported *H. scapularis* as an economic pest on rice, which was the first report of economic damage in North America.

Wilke (1924) gave a summary of literature, biology, and economic aspects of *H. griseola*. He called the insect "the gray barley fly."

Becker (1926) revised the species of *Hydrellia* of the Palearctic Region, figured the head and thorax of *H. griseola*, and briefly covered the literature of the species.

Essig (1926) applied to *H. scapularis* the common name "the rice leaf miner," which is used in this report.

Kreiter (1927) published a biology of *H. griseola* in Russia on barley, wheat, and oats, in which he described the various stages under the common name, "the barley fly."

Körting (1931) reared *H. griseola* in Prussia on several economic crops at various temperatures, and reported on nutritional studies. He used the common name, "the gray barley-mining fly."

Cresson's (1932) report on the taxonomic studies of *Hydrellia* from Europe and North America listed the European *H. modesta* as a variety of *H. griseola*. He also discussed the relationship of the European *H. incana* and *ranunculi* to the American *H. hypoleuca*.

Séguy (1934) revised the species of *Hydrellia* of France and figured the head and wing of *H. griseola*.

Balachowsky and Mesnil (1935) reviewed the literature of *H. griseola*, briefly described the adult and immature forms, and discussed the life history and economic importance.

Johannsen (1935) described and figured the puparium of *H. hypoleuca*.

Oettingen (1935) described and keyed the chief larvae that infest grasses of Northern Germany, including *H. griseola*.

Hennig (1943) summarized the knowledge of the immature forms of *Hydrellia*. He included generic and specific keys, and reviewed the literature.

Cresson (1944) published a synopsis of North American Ephydriidae in which he reduced *H. scapularis*, *hypoleuca*, and *obscuriceps* of Loew to varieties of *H. griseola*, and included a key to the North American species.

Berg (1950) reviewed the knowledge of immature forms of *Hydrellia*. He cited pertinent literature and gave descriptions and biology of species found in pondweed.

Séguy (1950) included *H. griseola* among species associated with ecological plant zones and their respective hosts.

Nepveu and D'Aguilar (1951) reported on the biology and damage of *H. griseola* on rice in France.

Parker *et al.* (1951-52) listed several parasites of *H. griseola* reared from rice leaves in Uruguay, South America.

Hennig (1952) reviewed the immature forms of the Ephydriidae, and included a key to the genera and literature review of the species.

Lange *et al.* (1953) reported on the control and biology of "the rice leaf miner" in California. Photographs of all stages and damage were given.

Kuwayama *et al.* (1955) published extensive investigations on the biology, ecology, morphology and control of *H. griseola* "the smaller rice leaf miner" in Japan, and figured adult and immature forms.

Féron and Audemard (1956) reviewed the life history, parasites, and control of *H. griseola* on rice in France.

Zangheri (1956) reported on the biology and control of *H. griseola* on rice in Italy.

TAXONOMY AND DESCRIPTION OF STAGES

The rice leaf miner, *Hydrellia griseola* (Fallen), is in the tribe Hydrelliini, subfamily Notiphilinae, family Ephydriidae, order Diptera.

Hydrellia is a large genus, as is shown by the appearance of at least 110 specific names in the literature of the past 150 years. It is a very homogeneous group and its species are difficult to separate. Its wide distribution and long taxonomic history have made the genus a subject of frequent investigations. Much of the older taxonomic work, however, utilized characters showing considerable variation. The latest taxonomic work completed on this genus in North America was published by Cresson (1944) with the following introductory statement, "This genus is one of the most difficult of the Ephydriidae and a more satisfactory classification of its species will

probably not be secured until a thorough study of the genitalia is made, as those organs show a great variety of forms."

The three varieties listed for *H. griseola* in North America intergrade so completely with respect to their originally distinguishing character of facial coloration, that a distinct separation cannot be made. Because of this intergradation in coloration, similarity in genitalic structures, exact habitat, and the same distribution, these varietal names appear to lack taxonomic value. Specimens from many localities of California were sent to W. W. Wirth of the United States National Museum throughout the course of this study. He has consistently determined them as *Hydrellia griseola* (Fallen), without a varietal designation. In this report, all descriptions and biological data are based on *Hydrellia griseola* and include the variations formerly separated into the varieties *hypoleuca*, *scapularis*, and *obscuriceps* of Cresson (1944).

A partial synonymy of the species is as follows:

Genus *Hydrellia* Robineau-Desvoidy 1830, Essai Myod., 2, p. 790.

Type species: *Notiphila griseola* Fallen, 1813. (= *Hydrellia communis* Robineau-Desvoidy). First known designation by Becker, 1896.

Hydrellia griseola (Fallen)

Notiphila griseola Fallen, 1813, Kongl. Svenska Vetensk. Akad. Handl., 34, p. 250.

Hydrellia communis Robineau-Desvoidy, 1830, Essai Myod., 2, p. 790. (Macquart 1835).

Hydrellia chrysostoma (Meigen), 1830, System. Besch., 6, p. 67. (? = *H. viridescens* Robineau-Desvoidy, 1830, Séguin, 1934).

Hydrellia griseola (Fallen). Macquart, 1835, Hist. Nat. Insectes, Dipt., 2, p. 590.

Hydrellia incana Stenhammar, 1844 (Cresson, 1932).

Hydrellia modesta Loew, 1860, Neue Beitr. Kennt. Dipt., 7, p. 23. (Cresson 1932).

Hydrellia hypoleuca Loew, 1862, Monog. Dipt. North Amer., pt. 1, p. 151.

Hydrellia obscuriceps Loew, 1862, Monog. Dipt. North Amer., pt. 1, p. 152.

Hydrellia scapularis Loew, 1862, Monog. Dipt. North Amer., pt. 1, p. 153.

Hydrellia griseola var. *modesta* Loew, Cresson, 1932, Trans. Amer. Ent. Soc., 58, p. 6.

Hydrellia griseola var. *hypoleuca* Loew, Cresson, 1944, Trans. Amer. Ent. Soc., 70, p. 166.

Hydrellia griseola var. *scapularis* Loew, Cresson, 1944, Trans. Amer. Ent. Soc., 70, p. 166.

Hydrellia griseola var. *obscuriceps* Loew, Cresson, 1944, Trans. Amer. Ent. Soc., 70, p. 167.

Adult

Descriptions are based on mounted and alcohol-preserved specimens. Alcohol preservation is necessary to retain the true shape of abdominal and genital segments. Color is retained on pinned specimens but is partially lost in alcohol preservation. A white, high illumination dissecting light was used while making descriptions and interpreting colors. In order to show maximum and minimum ranges, measurements were based on 25 specimens.

Female. (fig. 1) Head: antennae dark, third segment with a slight greenish tinge, arista with five to six branching hairs; frontal lunule and fronto-clypeal region finely punctate, most commonly golden but varying from shining white to yellow to gold to golden brown, bordered with five facials; palpi club-shaped, sericeous, yellow except dark base, with four setae on distal edge; eyes finely and densely pilose; vertex olivaceous brown, lesser ocellars and verticals strong, greater ocellars weak.

Thorax: dorsum olivaceous brown dissipating laterally to metallic blue-



Fig. 1. The rice leaf miner, *Hydrellia griseola* (female).



Fig. 2. The rice leaf miner, *Hydrellia griseola* (male).

green to gray ventral regions; anterior and posterior dorsocentral bristles forming a dorsocentral rectangle (Pl. 1, fig. 6) with long dimension transverse. Legs: femora metallic blue-green, tibiae dark gray, tarsal segments black except the inner side of the first which is covered with dense golden setae. Halteres lemon yellow. Wings: (Pl. 1, fig. 4) length 2.5–3.2 mm, hyaline, oval, costal vein extends up to the extremity of the median, cross veins well separated from one another, costa II nearly twice the length of costa III.

Abdomen: dorsal area of tergites olivaceous brown dissipating laterally to metallic blue-green, with numerous setae; sternites and terminal tergites

Plate 1. *Hydrellia griseola* adult structures.

Fig. 3. Ventrolateral view of female abdomen with extended ovipositor.

Fig. 4. Right wing.

Fig. 5. Ventral view of male abdomen with partially extended aedeagus.

Fig. 6. Dorsal view of thorax.

Fig. 7. Lateral view of phallus.

- 1) Eighth abdominal sternite. 2) Entrance to gonopore. 3) Anus. 4) Subcostal vein.
- 5) Radial vein. 6) Radial 2+5. 7) Radial 4+5. 8) Median vein. 9) Cubitus vein.
- 10) Costa II. 11) Costa III. 12) Aedeagus. 13) Phallobase. 14) Fifth abdominal tergite.
- 15) Sixth abdominal tergite. 16) Dorsocentral rectangle.

PLATE I

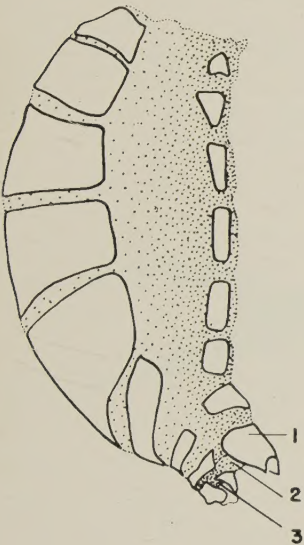


Fig. 3

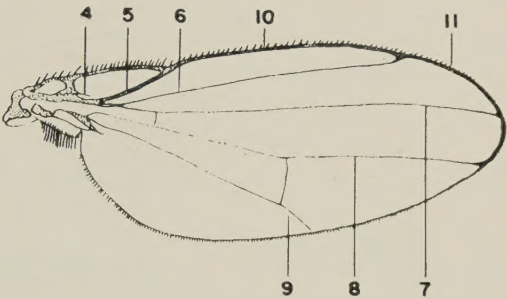


Fig. 4

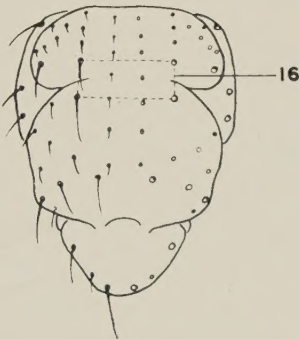


Fig. 6

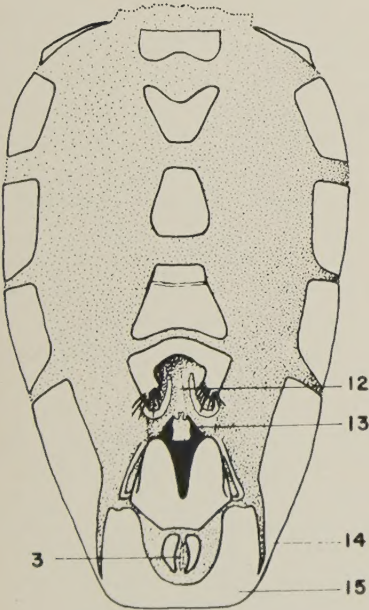


Fig. 5

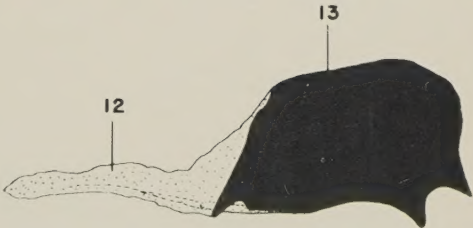


Fig. 7

PLATE 2

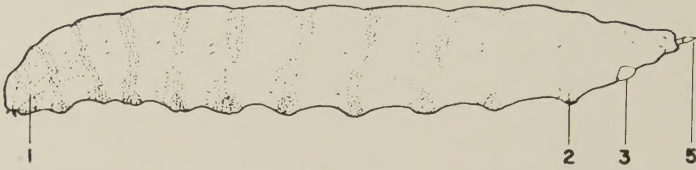


Fig. 8

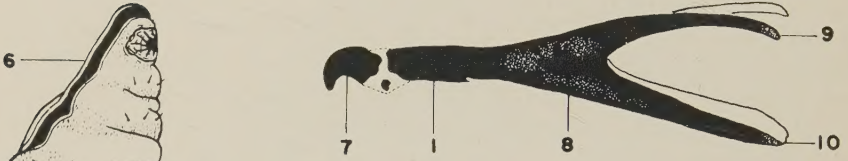


Fig. 10



Fig. 9

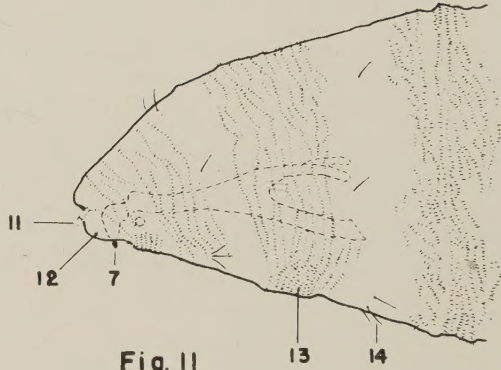


Fig. 11

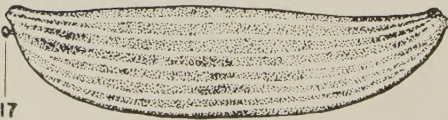


Fig. 12

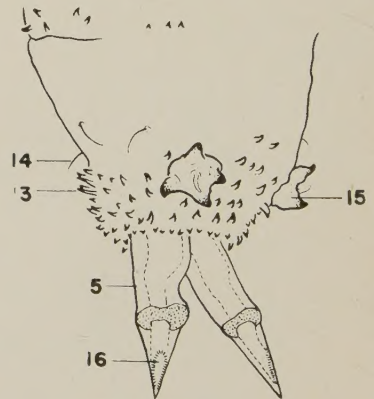


Fig. 13

shaped as in plate 1, figure 3, which are in an extended position. Total body length 2.0–2.8 mm, width 0.7–0.8 mm.

Male. (fig. 2) Under similar rearing conditions, male usually slightly smaller than female, otherwise similar to female except abdominal tergite V is broadly rounded apically; genital segments and sternites as in plate 1, figures 5 and 7. Total body length 1.8–2.7 mm, width 0.5–0.8 mm.

Egg

(Pl. 2, fig. 12) Measurement of 25 eggs gave the following size ranges: average length 0.66 mm, range in length 0.61–0.70 mm; average width 0.16 mm, range in width 0.15–0.17 mm. White, entire yolk mass opaque at time of laying, but posterior half turns yellow and anterior half shows black spiculi rings and pharyngeal skeleton of developing embryo; elongate, cylindrical; anterior end rounded and curved slightly away from leaf until curvature is interrupted dorsally by a projecting ridge; posterior end bluntly tapered and curved dorsally; chorion delicately sculptured with fine punctations and irregular longitudinal ridges which occasionally anastomose; micropyle terminal, consisting of a flattened head with flared lips and set on a short stalk.

Larva

(Pl. 2) General appearance and color were determined from living material, whereas measurements were taken from slide-prepared or alcohol-preserved specimens. With the exception of a few morphological characters and size, the three larval instars are nearly alike. The differences are given under their respective instars and unless otherwise indicated, the first and second instars can be considered similar to the third instar which is described in detail. Measurements of the pharyngeal skeletons and mouth hooks were based on 75 specimens and minimum and maximum measurements of larval instars selected from several hundred specimens.

First larval instar. Color nearly transparent to light cream when first hatched, but takes on a yellow to greenish tinge after feeding; length 0.33–1.13 mm; width 0.10–0.17 mm; pharyngeal skeleton 0.16–0.20 mm long; mean length of mouth hook 0.03 mm; dorsal region of postanal segment bearing two asteriform sclerotized structures (fig. 13) which may have two to five projections surrounding a seta.

Plate 2. Immature stages and structure of *Hydrellia griseola*.

Fig. 8. Lateral view of larva.

Fig. 9. Ventrolateral view of puparia.

Fig. 10. Pharyngeal skeleton and mouth hook.

Fig. 11. Lateral view of anterior end of larva.

Fig. 12. Lateral view of egg in normal position.

Fig. 13. Dorsolateral view of posterior end of second instar larva.

1) Pharyngeal skeleton. 2) Creeping welt. 3) Anal plate. 4) Anal slit. 5) Respiratory spine. 6) Dorsocephalo-thoracic cap. 7) Mouth hook. 8) Cheliform spot. 9) Dorsal rod. 10) Ventral rod. 11) Antenna. 12) Inferior tubercle. 13) Spiculi. 14) Seta. 15) Asteriform structure. 16) Tracheal orifice. 17) Micropyle.

Second larval instar. Color unchanged; length 0.82–2.17 mm; width 0.13–0.30 mm; pharyngeal skeleton 0.28–0.33 mm long, mean length of mouth hook 0.05 mm; asteriform structures on postanal region present and somewhat darker and larger than first instar.

Third larval instar. Color unchanged, internal organs and tracheae clearly visible; cylindrical and tapering at both ends (fig. 8); consisting of 13 segments: a pseudocephalon, three thoracic, eight abdominal and one postanal; length 1.67–3.40 mm; width 0.23–0.53 mm. Mouth hook and pharyngeal skeleton (fig. 10) black with slightly less pigment in area of cheliform spot and tips of dorsal and ventral rods; mouth hook of one piece, ventral rods fused, dorsal rods free; length of pharyngeal skeleton 0.43–0.50 mm, mean length of mouth hook 0.06 mm; mouth hook extends exteriorly through several lightly sclerotized processes or paraclypeal phragma surrounding the oral opening. Antennae (fig. 11) two-segmented, set on a small enlargement which may be a third segment; minute inferior tubercles ventral to antennae and just dorsal to tip of mouth hook (fig. 11). Anterior spiracles lacking; posterior spiracles (fig. 13) terminal on postanal segment. Anus opens ventrally through a slit in the anal plate (fig. 8) which is ovoid, slightly concave anteriorly and convex posteriorly, nearly three times as wide as long.

Anterior and posterior margins of dorsal segments (except 11 and 12) bearing numerous spiculi, irregularly arranged in transverse rows and confined to intersegmental furrows; ventrally, these spiculi form distinct, transverse, oval bands or creeping welts (fig. 8) on all except the pseudocephalon, anal and postanal segments. First two segments liberally covered with minute spiculi (fig. 11), anal segment bearing only a dorsal group of spiculi (fig. 8); postanal segment circled posteriorly with prominent spiculi (fig. 13), but no asteriform structure as in first and second instars. Anterior to and paralleling each creeping welt is a ring of ten setae, six confined to width of creeping welt and two on each side (figs. 8, 11); postanal segment bearing six setae.

Puparium

(Pl. 2, fig. 9) Measurement of 25 puparia gave the following sizes: average length 3.67 mm, range in length 3.10–4.25 mm; average width 1.01 mm, range in width 0.90–1.25 mm. Color, transparent light-to-dark golden brown. Ovoid, subcylindrical; posterior end tapering gradually to last segment which bears two terminal respiratory spines, curvature of posterior end quite variable. Anal plate ovoid, anterior margin convex, posterior margin only slightly concave. Anterior end of puparium gradually tapering on sides to a blunt tip, venter straight, dorsum sharply angled downward from fourth segment to tip, forming a dorsocephalo-thoracic cap. Pharyngeal skeleton of third instar larva remains in puparium; setal pattern as shown and described for larva.

DISTRIBUTION

A review of available literature shows *Hydrellia griseola* to be widely distributed throughout the Holarctic Realm. It has been reported from North

America, Europe, Asia, and Africa, but to my knowledge it has been limited within these continents to the Nearctic and Palearctic regions. A single reference (Parker *et al.*, 1951-52) reports it from the Neotropical Region in Uruguay, South America.

The fly's presence has been recorded in the following areas within the Palearctic Region: British Isles, France, Italy, Germany, Denmark, Poland, Norway, Sweden, Finland, Estonian S.S.R., Latvian S.S.R., Lithuanian S.S.R., Moldavian S.S.R., Ukrainian S.S.R., U.S.S.R. (European and Far Eastern Asiatic sections), Japan, Korea, and Egypt.

In the Nearctic Region, the known distribution of *H. griseola* extends as high as the 61st parallel (Alaska) and as low as the 27th parallel (Florida). It has been recorded from all the provinces of Canada except the Northwest territories, Yukon, and Newfoundland. Collections from 15 of the major museums of the United States report *H. griseola* from a total of 34 states. The collections contain no flies from Alabama, Arkansas, Delaware, Kentucky, Maine, Mississippi, Nebraska, North Carolina, North Dakota, Oklahoma, Rhode Island, Tennessee, Vermont, and West Virginia. All of these states have at least one bordering state with a record of *H. griseola*, indicating that further research probably will show it to occur in every state.

Examination of the specimens in California museums and in personal collections have revealed the presence of *H. griseola* in every county of California except Alpine, Del Norte, Imperial, Santa Barbara, and Sierra. It is probable that the species could also be found in these counties with additional collecting. Known vertical distribution of *H. griseola* in California extends from 282 feet below sea level (Badwater, Death Valley, Inyo County) to 8,500 feet above sea level (Sardine Creek, Mono County).

From the wide distribution presented, one might expect to find *H. griseola* anywhere in the Holarctic Realm, regardless of prevailing temperatures. It has a wide range of temperature tolerance in comparison with many other species of insects, but it is the author's opinion that the presence of fresh water, and suitable water temperatures is more important than general climatic conditions in limiting its distribution and establishment.

HOST PLANTS

All known species of the genus *Hydrellia* are leaf or stem miners; in fact, leaf mining in the family Ephydriidae is restricted to this genus. Members of this family typically live near the water, and the majority of the host plants of *Hydrellia* are aquatic or closely associated with water. A few species, such as *H. griseola*, have been able to make the transition from aquatic to terrestrial plants.

E. M. Hering (1951) reports that *H. griseola*, in Germany, normally occurs on aquatic grasses and shows a preference for *Phalaris* which grows on the edges of rivers and ponds. It frequently adopts the habit of attacking plants in fields located in river valleys and similar places. In these situations, it often attacks barley and has been considered a serious pest. It is a grain pest, however, only in damp areas in the vicinity of water. Other investigators confirm Hering's observations, as they report that *H.*

griseola is a serious pest only in the spring when cool, damp conditions prevail.

The occurrence of *H. griseola* as a pest of barley, oats, and wheat was reviewed by Wilke (1924), and Balachowsky and Mesnil (1935) who reported it from at least one of these economic crops in the following countries: Norway, Sweden, Finland, Germany, Denmark, Holland, France, Poland, Latvian S.S.R., Estonian S.S.R., Lithuanian S.S.R., Moldavian S.S.R., Ukrainian S.S.R., U.S.S.R. (European and Far Eastern Asiatic sections). These infestations were not of equal intensity in any one year or single locality, but appeared to be sporadic. Reports of damage caused by the larvae ranged from that of an occasional mine to nearly 50 per cent crop loss. Wilke (1924) stated that species of *Phytomyza* and *Agromyza* also mine these cereals at the same time as *H. griseola*, which has led to some confusion and may detract from the validity of some reports. Schøyen (1930) suggested that a considerable portion of the injury to oats attributed to *H. griseola* in Sweden was due to *Phytomyza avenae* Meij., which it closely resembled.

H. griseola does not seem to attack barley under field conditions in California. At Davis, young barley plants examined in late winter and early spring have consistently revealed no mines. Flies were taken at the same time in water traps, and other grasses were commonly attacked. I have found no records of *H. griseola* mining barley or wheat in North America under natural conditions. Records of the United States National Museum show one specimen reared from oats at Florence, South Carolina, in November of 1949. Under laboratory conditions, I have successfully reared *H. griseola* from all three cereals.

Velichkerich (1927) and Isaev (1931) listed *H. griseola* as a pest of onions in several European sections of the U.S.S.R., and E. M. Hering (1951) reared *H. griseola* from onions in his laboratory in Germany.

A review of the literature of the last twenty years revealed no serious economic infestations of *H. griseola* on barley, oats, wheat, or onions, but as a pest of rice it began to assume greater importance. Willecocks (1925) recorded *H. griseola* mining rice in Egypt. Minor infestations of rice occurred in the Far East Province of the U.S.S.R. according to Engel'hart (1936). Nepveu and D'Aguilar (1951) reported *H. griseola* as a new pest on rice at Camargue, France. Risbee (1952) and Féron and Audemard (1956) published on the continued presence of *H. griseola* in France. In North America, deOng (1922) first reported the rice leaf miner in parts of California. In 1933, Cartwright *et al.* found minor infestations in the rice fields near Sacramento, California. Lange *et al.* reported a 1953 outbreak of *H. griseola* in practically all the rice-growing areas of California. In Japan, Kuwayama *et al.* (1955) published investigations of *H. griseola* as a serious rice pest of the Northern Provinces. Parker *et al.* (1951-52) recorded the rearing of parasites of *H. griseola* which was mining rice in Uruguay, South America, but did not publish on the economics of the miner. Zangheri (1956) listed *H. griseola* as a new pest of rice in Italy.

The known host plants of *H. griseola*, arranged alphabetically by families and genera, are given in table 1. This list is a compilation of not only

TABLE 1
PLANT FAMILIES AND GENERA RECORDED AS HOSTS OF
HYDRELLIA GRISEOLA

Hosts	Europe	Asia	N. A.	Hosts	Europe	Asia	N. A.
Alismaceae				Gramineae (cont.)			
<i>Alisma</i>	X	X	X*	<i>Muhlenbergia</i>	X	..
<i>Sagittaria</i>	X	<i>Oryza</i>	X	X	X*
<i>Damonium</i>	X*	<i>Panicum</i>	X	X*
Caryophyllaceae				<i>Paspalum</i>	X*
<i>Lychnis</i>	X	<i>Phalaris</i>	X	X	X*
<i>Stellaria</i>	X	<i>Phleum</i>	X	X	..
Chenopodiaceae				<i>Phragmites</i>	X	..
<i>Kochia</i>	X	<i>Poa</i>	X	X	..
Compositae				<i>Polypogon</i>	X*
<i>Bellis</i>	X	<i>Secale</i>	X	X	X*
Cyperaceae				<i>Setaria</i>	X	..
<i>Carex</i>	X	X	X	<i>Triticum</i>	X	X	X*
<i>Cyperus</i>	X	X	X	<i>Zea</i>	X	..
<i>Scirpus</i>	X	<i>Zizania</i>	X	..
Gramineae				Hydrocharitaceae			
<i>Agropyron</i>	X	X	..	<i>Hydrocharis</i>	X
<i>Agrostis</i>	X	..	<i>Stratiotes</i>	X
<i>Alopecurus</i>	X	X	..	Labiatae			
<i>Anthoxanthum</i>	X	X	..	<i>Lamium</i>	X
<i>Avena</i>	X	X	X*	Leguminosae			
<i>Bromus</i>	X	X*	<i>Trifolium</i>	X	X	X*
<i>Calamagrostis</i>	X	..	Lemnaceae			
<i>Catabrosa</i>	X	<i>Lemna</i>	X
<i>Cynodon</i>	X	Liliaceae			
<i>Dactylis</i>	X	X	..	<i>Allium</i>	X
<i>Digitaria</i>	X	..	Polygonaceae			
<i>Echinochloa</i>	X*	<i>Polygonum</i>	X
<i>Eragrostis</i>	X	..	Scrophulariaceae			
<i>Festuca</i>	X	X	..	<i>Veronica</i>	X
<i>Glyceria</i>	X	..	Typhaceae			
<i>Hierochloa</i>	X	..	<i>Typha</i>	X*
<i>Holcus</i>	X	X	..				
<i>Hordeum</i>	X	X	X*				
<i>Lolium</i>	X	X	X*				

Europe: Brischke (1881); Grunberg (1910); Hering, M. (1924, 35-37); Hering, E. M. (1951); Kirchner (1906); Lilljeborg (1861); Linnanemi (1913); Nepveu, D'Aguilar (1951); Ruschka, Thienemann (1913); Séguy (1934); Ulmer (1928); Velichkerich (1927); Wilke (1924); Zangheri (1956).

Asia: Engel'hart (1936); Kuwayama *et al.* (1955).

North America: deOng (1922); Lange *et al.* (1953); Grigarick (present study); Malloch (1915); Webster, Parks (1913).

X indicates a host plant has been recorded in the genus.

* Reared or collected from the genus during this study, 1954-1956.

the available literature, but also records findings secured by the present studies. The genera listed represent both field collections and laboratory rearings, since the literature does not always state the origin of the material. There is also the possibility of wrong determinations of *Hydrellia* species, particularly by early workers at a time when ready taxonomic or biological references were unavailable. Certain authors have questioned the

validity of the genera *Hydrocharis*, *Stratiotes*, and *Lemna* as host plants of *H. griseola*, because other closely related *Hydrellia* species occur on them.

The most important family of plants serving as hosts of *H. griseola* is the Gramineae which contains nearly twice as many host genera as the remaining families. From a phylogenetic point of view, the 14 families listed in table 1 are widely divergent, a fact that appears to demonstrate the polyphytophagous nature of the miner. However, field observations and a literature review show the larvae to be at least ten times more prevalent on graminaceous plants than the remaining families. A primary reason for the wide range in host genera in divergent families is due to one of the larval habits. During the later stages of development, the larva may leave the mine to form a new one on the same or another plant. When the larva vacates an old mine, it does not appear to be too specific in the choice of another host. It may mine in the new plant for a brief period or immediately form a short blotch mine and pupate. For example—*Lychnis*, *Lamium*, *Trifolium*, and *Veronica* were host genera in which only short pupal mines were found.

The host list of *H. griseola* appears to suggest an ecological rather than a phylogenetic grouping. The main host family of the ecological group is the Gramineae. The families of secondary importance are those usually associated with the grasses by the common bond of an aquatic habitat or the occurrence of high moisture conditions.

LIFE HISTORY AND HABITS

This section discusses the life history and various habits of the different stages of *Hydrellia griseola*, arbitrarily starting with the adult. Laboratory experiments and field observations are combined to emphasize certain factors and show various ecological relationships. The section is introduced by an account of the techniques and equipment employed in the life history study.

Laboratory Methods and Equipment

Adults of *H. griseola* used for laboratory study were collected in the field by several methods. A small insect net was placed directly over flies on the water surface or vegetation within several inches of the water surface. (The usual method of sweeping with a standard insect net was unsatisfactory because of the specialized habitat and flight habits of the flies.) The adults were removed from the net by an aspirator and placed in a separate container. Aspiration of flies directly from the water or foliage was also applied if the adults were abundant. This method was faster and eliminated occasional injury incurred while handling in the net. Another method was to collect puparia and hold for emergence, but they were not always available in the quantities needed. The field-collected flies were anesthetized in the laboratory with carbon dioxide gas so they could be checked for species and sex before being transferred to permanent cages. A series of adults from each field collection and from each experiment were mounted in case a later species verification became necessary.



Fig. 14. Small and large adult cages.

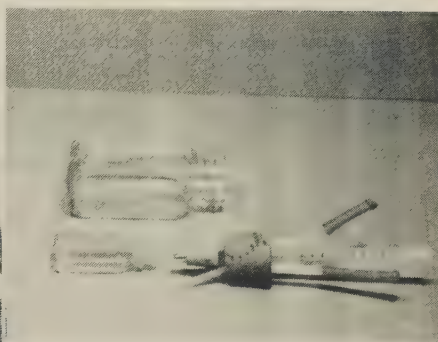


Fig. 15. Controlled temperature chamber used for adult activity study.

Two types of glass containers were used as cages for the flies. Small cages (fig. 14) were made from wide-mouth, quart canning jars with the bottoms removed to form a container $6\frac{1}{2}$ inches high and $3\frac{1}{2}$ inches in diameter. The inside lid of the canning jar was replaced by a 40-mesh brass wire cloth which was perforated to admit a feeding vial. The large cages were 1-gallon jars modified in a similar manner to form a container 8 inches tall and 6 inches in diameter. Both cages were placed in pans containing 1 and 2 inches of water, which was changed twice a week.

Controlled temperatures used in these studies were from several sources. Cabinets with bi-metallic thermostats utilizing an electric heat source of



Fig. 16. Constant humidity chamber (left) for adults and puparia.

Fig. 17. Constant humidity chamber for eggs (below).



light bulbs or resistance coils were used in addition to refrigerated rooms with vapor thermoregulators. Range of accuracy of this equipment varied from $\pm 0.5^\circ$ to $\pm 2.0^\circ$ F which is given in conjunction with the respective experiments. Temperature recording equipment was checked periodically with a standard thermometer which was in turn calibrated with a master thermometer of the weather station at Davis.

The apparatus shown in figure 15 was used for adult and larval activity studies at controlled temperatures. It consists of a small four-sided bottle with inside measurements of $1.5 \times 0.5 \times 0.5$ inches that fits inside a bottle $2.5 \times 2.0 \times 1.0$ inches. The desired number of flies or larvae were placed inside the small bottle and a cork inserted in the opening. A mercury thermometer ($\pm 1^\circ$ F) passed through the cork of the small bottle and into the chamber containing the specimens. The opposite end of the thermometer passed through the cork of the larger outside bottle so that it acted as a support which allowed the smaller bottle to remain suspended. Inlet and outlet plastic tubes were also placed through the large cork on each side of the thermometer. The inlet tube passed to an elevated, temperature-controlled, water-bath reservoir and the outlet tube extended to a lower drain. The apparatus was sufficiently small to enable observations with a binocular microscope.

Constant humidities were maintained by utilizing saturated salt solutions selected from a compilation by O'Brien (1948). The salt solutions were placed in sealed, 300 and 1,000 ml Erlenmeyer flasks shown in figures 16 and 17. A glass tube $\frac{1}{2}$ inch in diameter and 5 inches long projected through each outer rubber stopper to suspend the subject being tested over the solution. The 300 ml flasks were used in testing the eggs, which were placed in a small plastic dish. The dish was attached to a cork inside the suspended glass tube by a stainless steel pin. Microscopic examinations were made of the eggs by removing the plastic dish and pin. The 1,000 ml flasks were used for studies of the adults and puparia. Flies were confined within the flasks in shell vials $1\frac{1}{4}$ inches in diameter and $3\frac{1}{2}$ inches long. The bottoms were removed from the vials and replaced by 40-mesh brass wire cloth held in place by two rubber washers. The vial was held above the saturated salt solutions by a rubber stopper attached to the suspended glass tube. Adults were placed and removed by aspiration through the glass tube.

The sealed flasks were kept in constant temperature cabinets and the humidity inside the flasks was assumed to be what was reported for the chosen salt and temperature. The salts used in this study were K_2SO_4 , NaCl, $Ca(NO_3)_2 \cdot 4H_2O$, and $MgCl_2 \cdot 6H_2O$.

Adult

Habitat Preference. As previously mentioned, *H. griseola* adults exhibit a decided preference for high moisture areas. At certain times of the year, flies were collected near almost any body of water, but occurred in greatest numbers on calm water where vegetation was most abundant. That adults are not restricted to such areas is shown by the fact that they have occasionally been collected in alfalfa fields, pastures, oat and barley fields, and

even from apple blossoms. These collections, however, were made in the fall, winter, or spring months which are seasons usually characterized by cool temperatures and periods of greatest rainfall.

The environment occurring at temporary or permanent ponds, streams, and lakes provides the type of ecological niche most suited to breeding of this fly under natural conditions. Physical factors such as temperature and moisture, and biotic responses such as the choice of oviposition site, search for mates, and feeding habits all interact to establish the preferred habitat.

Emergence. Intermittent movement by the immature adult has been observed inside the pupal sack for 12 hours prior to emergence. The ptilinum plays the most important role in rupturing the pupal sack and forcing open the dorsocephalo-thoracic cap. The cap is nearly horseshoe-shaped and composed of the dorsal half of the first four anterior segments. Cleavage first occurs along the sides of the cap and lastly the anterior tip, while the posterior portion usually remains attached to the puparium. The corresponding ventral half of the puparium remains intact.

The head is freed first and the mouth parts are used to some extent by pushing backward against the ventral portion of the anterior tip of the puparium, until the first pair of legs is free. Once this occurs, emergence is rapidly completed. If the puparium is free of the leaf, the adult removes itself in one to two minutes, but it occasionally becomes wedged or entangled and dies while only partially out. If the puparium is within the pupation mine, it must also rupture the thin epidermis of the leaf. The break in the leaf tissue usually follows the longitudinal ribs, if it is in a grass blade, and the fly must then pull itself through this slit after once forcing its head through. When the leaf dries and the epidermis is not pliable, the adult is occasionally unsuccessful in this maneuver and remains trapped.

The newly emerged adult is light gray in color and quite soft and pliable. It walks briskly about and stops repeatedly to stroke and clean various parts of the body with its first and third pairs of legs. The ptilinum is occasionally inflated and deflated during this stroking procedure. The wings are contracted and folded along the longitudinal veins. After 10 to 15 minutes they are quickly expanded, but flight may not occur for 40 to 60 minutes. During the time between expansion and flight, the fly intermittently strokes its wings with the third pair of legs and the wings gradually become progressively firmer and darker in color.

The adults of *H. griseola* are hydrofuge, which readily enables them to crawl up emergent vegetation or bob to the surface if the pupation mine has sunk below the water level.

Emergence took place in the laboratory irrespective of the time of day or light conditions. Flies emerged at several constant temperatures between 50° and 90° F, but not at 43° F. More detailed information on humidity in relation to temperature and emergence is given in table 7 in conjunction with the section on pupal development.

Longevity. Adults used in the longevity experiments were kept in glass cages such as the type shown in figure 14. The cages were placed over water to conform with the habitat preference of the fly. A 10 per cent sucrose

solution was used as the main diet, but it was supplemented occasionally with 5 per cent yeast hydrolysate.

Newly emerged adults, kept at room temperatures varying from 49° to 76° F (October to April), remained alive over a range of one to five months with a modal life of three to four months. The maximum life span for a female under these conditions was 146 days and for a male, 133 days. At a constant temperature of 70° F, a fertile female lived 76 days and a virgin female 58 days. At a constant temperature of 43° F, one female lived 91 days.

Adults collected in the field at various times of the year and kept in the laboratory provided the following longevity data (maximum for both sexes): July, room temperature of 55° to 81° F, male—108 days, female—139 days; October, room temperature of 50° to 74° F, male—130 days, female—135 days; February, constant 70° F, male—54 days, female—49 days.

To demonstrate the combined effect of temperature and humidity upon the longevity of the adults, an experiment was designed to utilize temperatures approximately every 10° F ranging from 58° to 100° F. Four saturated salt solutions were used with each temperature to provide relative humidities of from 31 to 98 per cent. Flies collected from the field in March were held

TABLE 2
EFFECT OF TEMPERATURE AND HUMIDITY UPON LONGEVITY OF
FIELD-COLLECTED ADULTS

Temperature ° F	Relative humidity Per cent	Saturation deficit mm Hg.	Per cent mortality at stated time intervals (hours)*					
			3	6	12	24	36	48
100 ± 1.....	97	1.5	0	20	90	100
	76	11.8	30	100
	46	26.6	70	100
	31	31.9	100
90 ± 1.....	97	1.1	0	0	10	60	100	..
	76	8.7	0	10	70	100
	48	18.8	0	70	100
	32	24.5	20	90	100
80 ± 1.....	98	0.5	0	0	0	0	0	50
	76	6.3	0	0	0	0	0	80
	51	12.9	0	0	30	100
	32	17.8	0	10	50	100
70 ± 1.....	98	0.4	0	0	0	0	0	0
	76	4.3	0	0	0	0	0	10
	54	8.3	0	0	0	40	70	100
	34	12.0	0	0	20	50	80	100
58 ± 2.....	98	0.3	0	0	0	0	0	0
	77	2.8	0	0	0	0	0	0
	56	5.4	0	0	0	0	10	20
	34	8.1	0	0	0	0	10	10

* Each percentage is based on 10 flies (5 females and 5 males) collected near Davis in March.

24 hours in the laboratory with food prior to placement at the selected exposures. Five males and five females were placed in a 1,000 ml flask (fig. 16) for each replication. Mortality counts were made at 3, 6, 12, 24, 36, and 48 hours which were expressed in percentages in table 2. No food or water was placed inside the cages during the 48-hour exposure.

The results of table 2 show a progressive decrease in toleration as the temperatures rise from 58° to 100° F. At all the temperatures tested, longevity was longest at the highest relative humidity and shortest at the lowest relative humidity. An additional observation made at 72 hours for the 58° F exposure showed no mortality at 98 per cent relative humidity, 30 per cent at 77 per cent relative humidity, 60 per cent at 56 per cent relative humidity, and 80 per cent at 34 per cent relative humidity.

Each humidity reading in table 2 is accompanied by a respective saturation deficit for that temperature. The saturation deficit permits a more plausible interpretation of the results. For example, a relative humidity of 34 per cent at 58° F appears to act much slower than the 31 per cent relative humidity at 100° F. This action is accountable by comparing the two saturation deficits which show a difference of 23.8 mm of mercury. At comparable saturation deficits the effect of temperature on longevity is quite apparent.

No significant difference in mortality was noted between sexes.

Range of Activity as Limited by Temperature. A study of the effect of temperature on various adult activities was conducted by using the apparatus described in figure 15.

Five- to ten-day-old, laboratory-reared flies were used, which had emerged at 58° F in December. The experiment included five replications of six flies for each trial. The temperature was lowered to 28° F and then raised in increments of 2° every four to five minutes. High moisture conditions were maintained throughout the trials by wetting the cork stopper of the test chamber.

The results are averaged and summarized in table 3. Arbitrary descriptive phases of activity are placed opposite their respective temperature ranges. The phase of activity termed "heat rest," which occurred at 98° to 104° F, may be called "heat paralysis" by some authors. It is characterized by a general motionless state but differs from "heat paralysis" in that the flies retain coordination.

An equal number of males and females were used, but no sexual difference in response was noted. Recovery observations following exposure to sublethal temperatures of five minutes were based on six flies at each of the following temperatures: 108° F—full recovery in five minutes; 110° F—two-thirds recovery in two to three hours; 112° F—one-third recovery in two to three hours; and 114° F—no recovery.

Temperatures low enough to produce death within the prescribed time interval were not available. However, of 12 field-collected adults placed in a cotton-stoppered vial at 29° F ($\pm 1^\circ$), one remained alive a maximum of 42 days. The first died after 17 days and 50 per cent were dead in 34 days. Food was available during the test, but it is not known if feeding took place.

TABLE 3
TEMPERATURE RANGES SHOWING VARIOUS
PHASES OF ADULT ACTIVITY*

Temperature† ° F	Activity
110-114.....	Thermal death
107-110.....	Heat paralysis
104-107.....	Dropping
98-104.....	Heat rest
90- 98.....	Excitement
52- 92.....	Flight
52- 94.....	Jumping
51- 88.....	Normal walking
40- 50.....	Slow walking
28- 40.....	Slight upright movement

* Thirty equally sexed, 5 to 10-day-old, laboratory-reared flies were used.

† Temperature ranges were averaged from five replications.

Phototropic Responses. General observations of *H. griseola* indicate that it is positively phototropic. This knowledge was utilized in designing emergence cages and in transferring flies from one container to another.

Observations of the adults during the temperature-activity study suggested that a reversal of phototropism occurs at approximately 50° F. During these studies, part of the apparatus in which they were confined was occasionally shaded, and when the temperature was above 50° F, greatest activity occurred in the brighter section. Below 50° F, activity appeared to be directed toward the darker section. The apparent reversals were observed when the temperature was dropped below or raised above 50° F. The response was not complete, however, and movement was so slow that no definite conclusions could be formed.

A separate experiment was conducted with a larger sample of flies at two constant temperatures, one above and one below 50° F, and extended over a longer time interval. The flies were placed in 12 test tubes 6 inches long and 1 inch in diameter, which were stoppered with cotton plugs. Food and moisture were provided on paper strips which extended the length of the tubes. They were then placed horizontally through holes in the side of a box so that half of each tube was darkened and half exposed to a 100-watt light approximately 9 feet above. The box containing the tubes was alternately placed at $43 \pm 1^\circ$ F and $58 \pm 1^\circ$ F. Counts of flies in the light and dark areas were made at intervals of one to four hours, but length of exposure seemed to make no consistent difference in the counts after a one-hour period. Half of the replications were made with the cotton plugs in the darkened box and half outside. The averaged results in table 4 show that response was not complete to either the dark or light sections but occurred in the ratio of 7:18 positive to negative at 43° F, and exactly reversed to 18:7 positive to negative at 58° F. Additional temperatures greater and less than

TABLE 4

REVERSAL OF PHOTOTROPISM BY ADULTS AT SELECTED TEMPERATURES*

Trial number†	Number flies	Response		Number flies	Response	
		+	—		+	—
Temperature 43° ± 1° F				Temperature 58° ± 1° F		
1.....	39	11	28	47	37	10
2.....	50	8	42	50	36	14
3.....	55	22	33	53	34	19
4.....	50	15	35	50	39	11
5.....	57	15	42	57	44	13
6.....	39	11	28	47	35	12
7.....	47	20	27	53	48	5
8.....	57	18	39	57	39	18
9.....	57	7	50	57	33	24
10.....	57	16	41	57	37	20
Totals.....	508	143	365	528	382	146
Percentages.....	..	28.2	71.8	..	72.3	27.7

* Response was determined by the fly's presence in the light or dark half of 12 confining test tubes on a horizontal plane.

† The test tubes of the first five trials contained cotton plugs at the positive end which were reversed to the negative end during the last five trials.

the 7° to 8° range from the approximate 50° F reversal point may result in different ratios, but time and equipment precluded continuance of this phase of study. An advantage to adults seeking darkened areas in the field during cold weather may be the shelter they would receive from critical low temperatures.

Field observations indicated that flies were attracted to bright reflecting objects. Aluminum foil would soon attract adults when placed on the water surface so that the sun's rays were reflected across the water. It was also not uncommon to find an adult on or inside an automobile which was parked in the sun near a water source. The attraction to reflecting objects may be the result of a response to locate the reflecting surfaces of an aquatic habitat.

Food and Feeding Habits. The retractible feeding apparatus of the adult is somewhat similar to that of the housefly or blowfly. It has a rostrum, haustellum, and terminal oval disk. The oval disk consists of two lobes called labella, which fold together when the fly is not feeding but open and spread horizontally when taking up food. Seven more or less parallel, transverse ridges called pseudotracheae are clearly visible on each lobe when the labella are spread open. These pseudotracheae communicate to a central collecting channel which leads to the mouth cavity proper. A single row of spinelike processes or teeth lies external to each of the five central pseudotracheae of each lobe. Each row consists of 20 to 25 teeth approximately 0.025 mm in length. These numerous spines or teeth may be analogous to the type of prestomal teeth of the calliphorids or muscids.

If the mouth parts of *H. griseola* function the same as those of a blowfly, then food can be ingested in the three ways described by Graham-Smith

(1930): (1) it can suck up liquid food, filtering out the particles of larger size; (2) the prestomal teeth can be used to scrape or puncture selected surfaces, moistening them with saliva or with vomitus to produce an emulsion that is ingested; or, (3) using neither teeth nor filtration apparatus, the fly may suck up directly, thick liquids and small contained particles.

Flies have been observed on the water surface, feeding on dead spring-tails, psyllids, mayflies, dragonflies, and even members of their own species. Adults were often seen moving about over the water surface in search of food when the temperature was above 50° F and the wind calm. Movement was directed toward various floating objects which were manipulated with the fly's front legs and oval disk. Numerous contacts of this nature were made until a suitable food source was found.

The water surface tension acts as a trap to many insects that fall on, and partially break through it. These victims provide a ready food source and the flies may be expected to be found on nearly any insect in this condition. The insect on which the fly feeds apparently does not have to be dead as weak movement of the prey was noticed on several occasions in the field. Weakened laboratory flies were often attacked and forced into the water surface film by other *H. griseola*, which then began to feed if no resistance was encountered. Several adults may feed simultaneously on the same subject. On two occasions in the field, a fly was seen attacking a live springtail on the water. It would jump on and roughly attempt to hold the springtail with its legs and oval disk, but was unsuccessful in both instances.

A field test to determine a possible attractant was conducted with several types of food placed in containers which were floating on the water surface. Flies explored the media and appeared to feed on the following: banana flakes (dry and moistened), fish meal (moistened), raw hamburger, yeast hydrolysate (dry and a 20 per cent water solution), and a 5 per cent yeast hydrolysate-10 per cent sucrose solution. More flies seemed to be attracted to the last combination, but no strong preference was noted.

Caged adults in the laboratory were fed the combination of 5 per cent yeast hydrolysate-10 per cent sucrose solution or 10 per cent sucrose only. If the combination was used, the food had to be changed every two to three days because of fermentation.

The many examples of food that have been reported for adults of *H. griseola* would class it as a saprophagus feeder, but its food-getting habits may at times place it as a type of predator. Field observation indicates the success of its predatory actions appears to be limited to insects that have been previously weakened or disabled.

Locomotion and Dispersion. Adults of *H. griseola* move about by several methods. The flies were most often observed walking on the water surface and vegetation, or combining walking, short hops 1 to 2 inches long, and short flight.

Field-observed flight varied from a few inches to approximately 15 feet in distance at an altitude of 2 to 3 feet above the water. The flight path was neither flat nor straight, but appeared to consist of a series of short, darting, zig-zag arcs. No hovering was noted before alighting. Other types of flight patterns may exist but the small size and gray color of the fly

make observations in its natural habitat rather difficult. Flies released in the laboratory usually flew upward by the same arcing motion until reaching the 12-foot ceiling. Flight behavior of this type in the field would subject it to much stronger wind currents than those occurring along the ground, but such behavior was not observed in the field.

Flies resting on the water surface were moved by wind currents quite forcibly. A constant flying or hopping effort was necessary to oppose this drifting motion until a solid object was reached. Adults were often found in greater abundance on the downwind end of a pond or puddle.

Water currents of streams and canals were also noted to play a part in dispersal. Flies were occasionally observed resting on objects such as leaves that were floating downstream. There is also the possibility that the immature forms may be transported downstream with their uprooted host plants during spring floods. The puparia at times become free of decaying leaves and may float for several days, which would subject them to the action of wind and water currents.

Copulation. The act of mating has been observed in the field between temperatures ranging from 55° to 90° F and during nearly any daylight hour. The season or degree of sunlight did not appear to be a factor as the act has been viewed every month of the year and during dark, overcast or bright, clear days.

In the laboratory, the time between emergence of females and the first known coition with males of the same age was three days. Pairs were often observed copulating 15 to 40 days after emergence, and in one instance mating was noted 70 days following emergence. The act was known to take place several times a day with a single pair of flies and has been observed through five consecutive days. Continuous mating, however, is apparently not necessary as one female laid fertile eggs 93 days after being isolated. One male is capable of fertilizing at least three females.

Copulation was observed most often on the water surface and floating leaves, but also occurred on upright foliage and the bordering shoreline. When a male and female are approaching each other, they often flex their wings upward and apart, a habit which is a rather consistent part of their premating behavior. A receptive female spreads and elevates her wings so the male may assume a position from behind and astride the abdomen of the female at an angle approximately 45° to the longitudinal plane of her body. The wings of the male remain folded over his abdomen, while the first pair of his legs extend forward so that the tarsi hook around the costal vein of the wings of the female, near her thorax. His second and third pair of legs extend backward on each side of the abdomen of the female, or the third pair of legs may touch the substrate. The male's abdomen is then brought downward and forward to connect his copulatory organs with those of the female. The female may remain motionless or continue to walk, hop, or fly short distances while *in copula*. The female terminates the act by raising her third pair of legs and forcing the male backward. Flies have been observed to remain in coition from one to 50 minutes.

Oviposition. Females observed ovipositing in the field showed a decided preference for leaves lying directly on or within a few inches of the water

surface. Eggs have been found 6 to 8 inches above the water level, but this usually occurred only on foliage which was very dense and subject to high humidity conditions. The favored site for oviposition was a leaf lying horizontally, but eggs were frequently laid on foliage in a vertical position.

Females were apparently able to distinguish between the face and back of the leaves of graminaceous plants, as the vast majority of eggs were found on the leaf face. After selecting a leaf, the fly would orient herself so that her anterior-posterior axis would parallel the longitudinal axis of the leaf. The tip of the abdomen was drawn along the leaf and a single egg was deposited longitudinally between or on the leaf ribs which coursed the length of the leaf. Generally several eggs were laid in this manner as the fly moved forward. Only rarely were eggs found with their longitudinal axis other than parallel to the leaf ribs. Eggs were also infrequently found on grass stems. A secretion was on each egg which firmly adhered it to the leaf.

Grass blades have been observed in the field with one to 52 eggs on them. The number of eggs already present on a leaf blade apparently was no deterrent to subsequent oviposition as females were occasionally observed to lay additional eggs directly on top of those present. The position of the leaf in relation to the water surface and the plant species seemed to be the most important factors governing the oviposition site. Oviposition has been observed in the field every month of the year, but only when the temperature was above 50° F.

In laboratory oviposition tests, newly emerged females were caged with males of the same age. The first oviposition started after five days at a room temperature that varied from 54° to 72° F. The egg-laying abilities of individual females varied considerably and no general conclusions could be made regarding egg number, frequency, or interval. Some of the factors that may have contributed to the variation, were age of the female, cage conditions, temperature, and diet. The yeast hydrolysate appeared to have a stimulating effect on oviposition. One female stopped oviposition, and was isolated and fed only 10 per cent sucrose for 108 days, during which time no eggs were laid. When five per cent yeast hydrolysate was again added to the food, she began laying viable eggs three days following the food supplement.

A summary of the maximum number of eggs laid at various time intervals for field-collected individuals which were held at 72° F, is as follows: 18 eggs in two and one-half hours, 28 eggs in 24 hours, 40 eggs in 48 hours, and 70 eggs in five days. The longest number of consecutive days in which eggs were laid was five. The maximum number of eggs laid by one female at 72° F was 199 over a 60-day period. The maximum number laid at 58° F was 73 in 52 days. At room temperatures of 62° to 92° F, 152 eggs were laid in 55 days. A virgin female started ovipositing eight days after emergence and laid 58 eggs over a period of 25 days, but the eggs were not viable.

Controlled temperature studies showed that oviposition could take place at temperatures ranging from 50° to 90° F. No oviposition occurred at 43° F. Tests conducted with controlled humidities proved inconclusive and contradicted field observations. Grass blades were inserted in the 1,000 ml flasks (fig. 16) which contained the selected humidities. At 90° F, oviposition took

place in flasks containing 35, 48, 76, and 97 per cent relative humidities. The placement of grass blades in the sealed containers added a source of moisture which probably upset the equilibrium of the system, and the relative humidity at the leaf surface may not have been the same as that predetermined for the selected salt.

Field observations showed certain grasses to be highly preferred to others as oviposition sites. Under similar conditions, eggs were usually very abundant on *Polypogon monspeliensis*, but less so on *Echinochola crusgalli*. These two plants were simultaneously exposed to 20 females in the laboratory. An equal number of leaves were arranged horizontally on water so that humidity would not influence oviposition. From a total of 146 eggs, 81 eggs or 55 per cent were laid on *E. crusgalli* leaves, and 65 eggs or 45 per cent were laid on the leaves of *P. monspeliensis*. A slight oviposition preference was indicated for *E. crusgalli* (contradicting field observations), but this preference did not prove to be statistically significant.

Laboratory females oviposited on all the genera of the North American Gramineae listed in table 1 except *Paspalum*, which was not offered. Oviposition also occurred on the sides of the glass cage when leaves were absent.

Egg

Incubation Under Controlled Temperatures and Humidities. Eggs of *H. griseola* were found throughout the year in certain areas in the field. Their position on the host plant and relationship to water has been discussed previously in conjunction with oviposition.

A laboratory study of incubation pointed out the importance of the maintenance of high moisture for completion of egg development. Eggs were subjected to seven constant temperatures, ranging from 43° to 100° F. Three different humidities were used at each temperature. The eggs were kept in 300 ml constant humidity flasks (fig. 17) which contained selected saturated salt solutions. Adults were allowed to oviposit on grass blades for a two-hour period. After egg deposition, the blades were removed and trimmed so that a minimal amount of leaf tissue remained attached to individual eggs. It was necessary to leave each egg attached to a part of the leaf, as attempts to remove the egg would often result in injury. The attached leaf tissue was cut to a minimum so that it would not unduly influence the predetermined humidity.

Movement of the first instar larvae was often observed within the egg several hours previous to emergence. The larvae would occasionally break the egg chorion but remain in the egg either permanently or from several minutes to hours before crawling out. This action occurred most frequently at critical exposure periods. Egg development was not recorded as complete until the larva had vacated the egg. Examination for hatching was made every two hours.

The results given in table 5 show that hatching occurred at temperatures ranging from 43° to 90° F, at a constant relative humidity of 98 per cent. Embryonation occurred in varying degrees at all temperatures and relative humidities tried except 48 per cent at 90° F. Eggs also failed to embryonate at a constant temperature of 100° F at relative humidities of 45, 76, and 97

TABLE 5

EGG DEVELOPMENT IN RELATION TO TEMPERATURE AND HUMIDITY*

Temp. ° F	R.H. Per cent	Sat. deficit mm Hg.	Incubation period in days			Per cent embryo- nated	Per cent hatched	Expo- sure†
			Minimum	Maximum	Mean			
90 ± 1.....	97	1.1	1.9	2.0	1.9	100	80	2
	76	8.7	2.0	...	2.0	100	10	17
	48	18.8	0	0	(38+)
80 ± 1.....	98	0.5	2.1	2.3	2.3	90	90	1
	76	6.3	2.4	2.8	2.6	80	40	16
	51	12.9	100	0	(34+)
72 ± 2.....	98	0.4	2.7	3.0	2.9	90	90	1
	76	4.8	3.6	4.2	3.9	100	40	19
	54	9.2	90	0	(36+)
58 ± 2.....	98	0.3	7.1	8.2	7.5	90	90	2
	77	2.8	7.6	...	7.6	100	10	21
	56	5.4	90	0	(41+)
50 ± 1.....	98	0.2	16.1	19.9	17.8	90	80	4
	77	2.1	80	0	(38+)
	59	3.8	100	0	(68+)
43 ± 1.....	98	0.1	35.5	38.0	36.8	90	90	4
	76	1.7	80	0	(63+)
	62	2.7	80	0	(99+)

* Each sample consisted of 10 eggs.

† Exposure is designated as the product of the mean incubation period and the saturation deficit. Parentheses indicate the use of the mean time of incubation of the next highest sample at which hatching occurred.

per cent. At least 10 per cent of the eggs hatched in constant humidities of 76 or 77 per cent at 58°, 72°, 80°, and 90° F, but no hatching took place in the same humidities at 43° or 50° F. An interpretation of these results by means of the respective saturation deficits alone is no more enlightening than by relative humidities. However, the product of the saturation deficits and the mean time of incubation listed under the column titled "exposure," presents a more plausible explanation. If a saturation deficit exists in the presence of a source of moisture (the egg), then in addition to the intensity of the deficit, the period through which it exists should be considered. The exposure figures indicated that a number over 5 to 10 was detrimental to the eggs and over 22 to 34 was fatal. Unfortunately, these saturation deficits and development temperatures did not fall frequently enough within the critical range so that a definite 50 per cent mortality point could be determined, if such a point exists.

The major reason eggs failed to hatch was assumed to be the various unfavorable combinations of temperature and humidity. Other factors may have acted adversely on the egg, as 100 per cent embryonation did not always occur at moderate temperatures and high humidities. All eggs used in the test were assumed to be fertile, as it was ascertained that unfertilized eggs collapsed soon after being laid. The hatching percentages calculated from

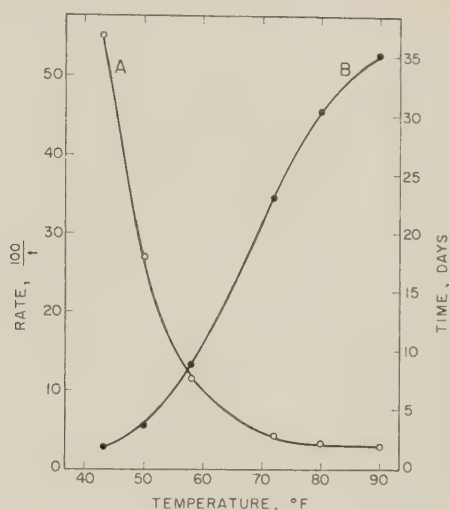


Fig. 18. Egg development through mean time of hatching at different temperatures and a relative humidity of 98 per cent. A, time-temperature curve; B, rate-temperature curve.

the number which embryonated instead of the original sample, would be slightly higher for some samples, but would show the same general trend.

The duration of incubation at 72° and 80° F was noticeably longer in the lowest humidities at which hatching occurred, but was undiscernible at lower temperatures because of mortality.

Mean development times were taken from table 5 and plotted against their respective temperatures at 98 per cent relative humidity to show a time-temperature or growth curve, A, in figure 18. The accompanying rate of development curve, B, was expressed at $100/t$ (where t = time required for development through hatching) and signifies the mean of the total development time completed per unit time at any given temperature. This rate, so calculated, is only the mean rate and is strictly a time expression. If the rate of development curve were expressed as a straight line by the method of least squares, it would show a theoretical zero of 43.9° F. Equipment was not available to determine the true threshold, but experimental results showed completion of egg development at 43° F, which is slightly below the theoretical zero.

A limited experiment was conducted to determine if the eggs could tolerate a subfreezing air temperature. Eighty eggs were put in a sealed quart jar (with moistened blotting paper) and placed at 29° F ($\pm 1^\circ$), two hours after they were laid. Ten eggs were removed from this group every 24 hours and placed at 80° F. Eighty per cent hatched after a 24-hour exposure. Twenty per cent hatched after 48, 72, 96, and 120 hours but no hatch occurred at or after a 148-hour exposure. The results showed a limited tolerance of the eggs to subfreezing air temperatures even though prolonged exposure was fatal.

To determine if water submergence was a limiting factor for egg hatching, a sample of 10 eggs on a leaf was submerged several inches below the water surface at a constant 80° F. All 10 eggs hatched after the normal incubation period and commenced mining, which indicated occasional flooding in the field may not be detrimental.

Larva

Mining. The larvae of *Hydrellia griseola* are classified as permanent miners. Their entire larval life is restricted to feeding on the mesophyll of plant tissue between the upper and lower epidermal layers, except for the time during which the larvae may occasionally change mines.

The larva emerges from the micropile end of the egg by rupturing the chorion with its mouth hook and the mine generally begins at the same end. Thus, the anterior part of the larva may be partially within the mine while the posterior section is still within the chorion. Conditions intervening since oviposition may have caused that section of the leaf to be unfavorable for mining. If such occurred, the larva moves about until a suitable section of the leaf or of a closely adjoining leaf is found and mining begins. In the laboratory, larvae that hatch from eggs which have been removed from leaf tissue will randomly test the various substrata they may contact until they die.

The larva penetrates the leaf epidermis and starts mining in cells of the parenchyma. The width of the early mine is 0.1 to 0.2 mm wide and is usually linear, although it may completely reverse direction or show some curvature. At this time the mine appears as a whitish streak across the leaf when viewed by reflected light. By transmitted light, it is visible from either side of the leaf as a thin green line, somewhat lighter in color than the surrounding tissue. The mine extends in a linear fashion for about half the larval life and gradually widens as the miner matures. Toward the latter half of development the mine may take on a blotchlike appearance as the larva moves up and down the sides of the mine and excavates an increasing amount of tissue. Mining may be concentrated in the upper or lower parenchyma during early development but there appears to be no consistency. The nearly mature larva completely excavates the inner leaf tissue so that only the upper and lower epidermal layers remain. These layers may rise somewhat similar to a blister and the bulge of the larva is easily observed or felt by sliding the leaf between the fingers. At this time, the mine is clearly visible from either side of the leaf by reflected or transmitted light.

The majority of mining activity is confined to the leaf proper, but now and then larvae are found in the leaf sheath and the stem. The greater number of mines occur in leaves lying on the water surface or a few inches above it, but they have been found 6 to 12 inches above the water, particularly when the air temperatures are low. Mining occurred occasionally in submerged leaves, but this was usually after a rain or irrigation had raised the water level.

The larval excrement or frass was left in the mine and no apparent order of disposal was noticed.

Movement. Locomotion by the larva is accomplished by coördinated movement of several body parts. The movement is the peristaltic-type in which the oral hook, creeping welts, respiratory spines, and muscles of the individual segments are employed together, or in various combinations, to produce specific acts.

The oral hook moves in rapid, short, semicircular arcs that are directed

laterally or ventrally. The hook penetrates the epidermis of the leaf in this manner and continues to excavate. As the excavated area is enlarged, the hook is anchored in the leaf tissue and the anterior segments are pulled within the mine. Very little or no pushing action is required from the respiratory spines or the posterior segments after the first few anterior segments are within the mine. This became apparent when several larvae, in the process of entering a leaf, were viewed in a vertical position or perpendicular to the leaf surface. The entrance hole is generally smaller than the width of the larva and each segment is constricted as it is pulled within the mine.

At 80° F, first instar larvae take two to two and one-half hours to complete their entrance from the egg into the mine. Third instar larvae require one-half to one and one-half hours to enter a new mine. Once within the mine, all sides of the larva are in close contact with the plant tissue and the setal rings and particularly the creeping welts are used as anchoring points in the semifluid environment. The body moves forward by a series of contractions appearing as waves from the posterior to the anterior. The mouth hook may pull to aid this movement and the respiratory spines appear to push as they are inserted in the plant tissue. Direction can be reversed by causing the contractions to run from anterior to posterior in which case the oral hook is used to help push the insect backward. The larva can also reverse its direction within the restricting mine by bending the body into a narrow U-shape.

Periodically the larva excavates, feeds, and rests within the original mine and continues this rhythm until development is complete. Occasionally it must migrate to a different leaf and start a new mine. This migration can take place at any instar. Some of the possible reasons for this change of mines are decomposition of the leaf, drying, unfavorably high temperatures, flooding, consumption of available food supply, or migration for pupation. Crowding often occurs during high populations, for as many as 15 to 30 first instar larvae have been found mining in a single field-collected leaf of grass. The individual mines are soon extended until only a single collective mine exists by necessity. A single leaf would rapidly become devoid of mesophyll tissue under these conditions and migration by the larvae become imperative. It was not too uncommon, however, to find three to five puparia in a single leaf.

Since the larva is subject to desiccation when it leaves the mine, it tends to avoid direct sunlight. One larva, observed in the field when the air temperature was 92° F, accomplished this by crawling from the dorsal to the ventral surface of a rice leaf which was lying on the water. Then, while submerged, it entered the leaf on the shady side. Larvae have often been observed in the laboratory to move across several inches of water by holding on to the submerged side of the surface film.

Several third instar larvae were placed in Petri dishes on damp sand and moistened soil to observe movement outside the mine. They moved readily about, apparently in search of a leaf until they either pupated or died. One larva moved intermittently for seven days before it died. The movement outside the mine is of the same peristaltic type, but the oral hook and respiratory spines appear to be used to a lesser degree and only the creeping welts

on the venter of the larva are in contact with the substrate. Exposed larvae that begin to dry will partially coil or twist their bodies and roll laterally, which is a much faster movement than the normal crawling.

Respiration. Larvae of all known *Hydrellia* are metapneustic. The only spiracles are slits that open near the tip of two hollow, pointed spines at the posterior end of their bodies (Pl. 2, fig. 13). These spines are frequently inserted in plant tissue and presumably are used to obtain oxygen from the intercellular gas spaces, as well as the air spaces that may exist in the mine. Larvae that are being reared in the laboratory would occasionally fall into the water while changing mines. They would attempt to crawl up the sides of the container, but would often be unsuccessful and drown. Submerged larvae that crawled along the under side of the water surface film would repeatedly force their pointed spiracles through the film, which appeared to indicate a search for oxygen.

The characteristic action of the spiracles and the drowning of the larvae indicate that absorption of oxygen through the body integument does not take place or is insufficient to support a strictly aquatic existence.

Molting. The body size and the dimensions of the pharyngeal skeleton of the three larval instars are given in the section on taxonomy.

The cuticula and pharyngeal skeleton are shed at the completion of the first and second instars while the larva is within the mine. These parts are readily found by opening the mine and are sometimes visible through the outer leaf surface. A larva in the process of molting is easily recognized by its state of inactivity. The new instar is creamy white and visible within the larger, fully extended cuticula of the previous instar. Exit from the old cuticula occurred at the anterior end, and the exuviae was rolled or pushed backward as the new instar crawled forward through the mine. The pharyngeal skeleton may become separated from the cuticula while they are being shed but they are usually found together.

The cuticula of the third larval instar forms the pupal case and it may be found within or outside the mine. The pharyngeal skeleton of the third larval instar is visible within the puparium.

The time between each larval instar varies with environmental conditions. At 80° F, approximately two to three days are equally spent at each instar. Food appears to be important, as well as temperature, in determining the time spent in each stadium.

The Pupation Mine. The third instar larva will often migrate to form a new mine prior to pupation. The size of this mine is quite variable, but usually occupies an area three to six times the size of the puparium. In a wide leaf, the pupation mine is usually blotch-shaped but it will occupy the entire width of the leaf and appear rectangular in a narrow grass blade. The location of the mine in relation to the plant tissue layer is quite constant. If the leaf is thin, all the mesophyll tissue will be mined so that only the epidermal layers will remain on either side of the puparium. The mining of the larvae will be limited to one side of a thick leaf, so that the puparium will have at least one side in contact with the epidermis. This procedure insures the future adult a minimum amount of plant tissue to penetrate, since no special opening is provided by the larva. Little or no frass is found in the pupation mine.

After completing the mine, the larva usually moves toward the center of the excavation to pupate. The respiratory spines are inserted into the plant tissue, which provides anchorage and perhaps serves a respiratory function. A small amount of dark substance is often observed at the junction of the posterior tip of the puparium and the leaf. Presumably, this is a secretion from the anal orifice which is characteristic for many types of miners and provides additional adherence to the leaf. Once the larva has established itself in this manner, it gradually shortens, thickens, and begins to darken as it takes on the typical shape of a puparium.

Pupation normally takes place in the leaf as just described, but attachment to the leaf is not absolutely essential. In the laboratory, third instar larvae have pupated on moist soil, sand, blotting paper, and glass. Occasionally a larva burrowed inside blotting paper and pupated. Leaves were either absent or dead at the time of these examples of pupation. It was not uncommon to find puparia, free of leaves, on the soil at the edges of streams or ponds. These may have floated to the edges from decomposed leaves, as well as from larvae falling from plants and completing pupation on the soil. Stormer and Kleine (1911) in Germany and Kuwayama *et al.* (1955) in Japan, have reported finding *H. griseola* puparia in the soil.

Third instar larvae, which had been separated from their host plant, were usually able to pupate unless they were just beginning the third instar. However, the puparium and emerging adult were generally smaller than normal or emergence often failed to take place.

Effect of Temperature on Activity and Longevity. Limited studies were made on the effect of gradually increasing temperatures upon larvae by using the same apparatus (fig. 15) that was used to study adult activity. First and second instar larvae were too small to be accurately observed by this method, consequently only third instar larvae were used.

Observations were made on two replications, each beginning with five laboratory-reared larvae that were mining in a single blade of beard grass. The temperature was lowered to 36° F and then raised, in 2° increments every four to five minutes, to 112° F for the first trial, and to 114° F for the second trial. The leaf was moistened so that the humidity within the observation chamber was high.

Activity at various ranges of temperature (averaged from the two replications) occurred as follows: 36° to 50° F, movement was stopped or was very slow; 50° to 90° F, movement and mining normal; 95° to 103° F, larvae moved about in a rather quick or agitated manner and some left the mines and moved about the test chamber; 104° to 111° F, very little or no movement occurred and the larvae appeared to be in what could be called heat paralysis; 112° to 114° F, thermal death. Two of the five larvae of the first replication recovered after being exposed to 112° F, but no recovery occurred at 114° F.

The effect of prolonged, constant high temperatures upon the larvae was observed by placing 10 of each of the instars, which were mining in beard-grass, at a constant 100° F and 104° F. The leaves that contained the mining larvae were placed on ½ inch of water in closed Petri dishes, so that the humidity remained high throughout the test. Exposure of 30 larvae (10 of each instar) to 100° (+ 1°) F showed the following mortality percentages:

12 hours—first instar 50 per cent, second instar 40 per cent, third instar 20 per cent; 24 hours—first instar 70 per cent, second instar 80 per cent, third instar 100 per cent; 48 hours—all dead. Five larvae had left their mines by 12 hours, 13 by 24 hours, and 15 by 48 hours. Exposure of an additional 30 larvae (10 in each instar) to $104^{\circ} (\pm 1^{\circ})$ F provided the following mortality percentages: two hours—no mortality; four hours—first instar 70 per cent, second instar 50 per cent, third instar 40 per cent; six hours—first instar 100 per cent, second instar 80 per cent, third instar 90 per cent; eight hours—all larvae were dead. Nine larvae left their mines in the first two hours, but this number did not increase with longer exposure. Mining was stopped when the larvae were placed to 104° F and it was necessary to touch them and force movement in order to determine mortality.

Prolonged exposure of larvae to subfreezing temperatures presents the problem of mechanical injury due to the freezing of liquids within the mine. Some larval mines are filled with liquid from ruptured cells, while others are only moderately damp. Leaves, that were being mined by 10 larvae of each instar, were placed on moistened blotting paper, inside closed Petri dishes, at $29^{\circ} (\pm 1^{\circ})$ F. After an exposure of 24 hours, 20 per cent of the first instar larvae were dead, 70 per cent of the second instar, and 80 per cent of the third instar. When the survivors were exposed an additional 24 hours, two first instar larvae were still alive but all third and second instars were dead. A third exposure of 24 hours killed the remaining first instar larvae. A second test of 10 first instar larvae showed 100 per cent mortality in 24 hours, which conflicts with the first test but points out the variability which is probably due to the amount of liquid that froze in the individual mines. The tests do indicate, however, that if conditions within the mine permit, there is a limited degree of tolerance at this subfreezing temperature.

Development in Relation to Temperature. Larvae have been found mining throughout the year when host plants were available in suitable locations. Detailed information concerning these locations and the numerous conditions that affected mining in the field are discussed in a later section. Temperature was found to be an important factor governing the rate of development and mortality in both the field and the laboratory.

Equipment for growing plants under a range of controlled temperatures was not available. The ability of the larvae to readily change mines was utilized, however, so that development could be observed in constant temperature chambers. Eggs, laid (within a two-hour interval) on leaves of *Polypogon monspeliensis*, were placed on the surface of 1 to 2 inches of water in a porcelain enameled pan $3\frac{1}{2}$ inches deep and 7 inches in diameter. An identical pan was inverted and placed over the pan containing the eggs, to maintain a humidity near saturation. The eggs were examined periodically until a mean time of hatching could be determined. Fresh blades of *P. monspeliensis* were cut and placed on the older leaves that were being mined. These fresh leaves were always made available so that the larvae could migrate from decomposing leaves and resume mining. The blades were examined every four hours upon commencement of pupation and the puparia were recorded and removed.

Results of the study at temperatures of 50°, 58°, 72°, 80° and 90° F are given in table 6. Larvae failed to complete development at 100° F. A maximum number of 82 per cent pupated at 72° F and a minimum of 50 per cent at 50° F. However, pupation percentages may not reflect a true indication of the effect of temperature because of the artificial conditions of rearing. The greatest mortality appeared to be by drowning, as larvae were often found under water at the bottom of the pan. This presumably occurred when the larvae fell from a leaf while making a transfer to a new leaf. Some of the larvae were observed to crawl up the wall of the pan and again start mining on the leaves at the water surface.

TABLE 6
LARVAL DEVELOPMENT IN RELATION TO TEMPERATURE*

Temperature ° F	Number of larvae	Length of larval stage, in days			Per cent pupated
		Minimum	Maximum	50 per cent	
90 ± 1.....	45	5.1	9.3	6.9	57
80 ± 1.....	82	6.5	9.6	7.6	70
72 ± 2.....	88	7.2	12.9	8.1	82
58 ± 2.....	101	18.5	25.9	21.1	78
50 ± 1.....	80	33.5	49.4	41.0	50

* Host plant, *Polypogon monspeliensis*.

The period of time between the first and the last miner to pupate at each temperature increased with a decrease of temperature except at 90° F. At this temperature, the interval was longer than at 80° F, which indicates that a temperature this high may have a retarding effect upon completion of growth. The time interval between the first and last pupation, at all temperatures, is longer than one would expect in normal growth variation, and may be due to nutritional differences. Fresh leaves were always available for larval migration, but throughout the studies it was often noted that some larvae would quickly transfer while others would remain in leaves that were quite yellow. After five days at 80° F, the majority of larvae were in the second or third instars. A few first instar larvae, however, were still present in the yellowed leaves on which the eggs were originally laid. The chemical changes that occurred in the decomposing leaves may have decreased the nutritive value of the food and thus lengthened the time of development. The number of transfers to new leaves may also have delayed the completion of larval development, but the use of a mass-rearing technique precluded a detailed check on migration.

The times at which 50 per cent of the larvae pupated were taken from table 6 and plotted against their respective temperatures, to present a growth or time-temperature curve, A, in figure 19. A rate of development curve, B, is also given, which is expressed at $100/t$ (t = time required for development of 50 per cent of the larvae up to pupation). The rate of development curve expressed as a straight line by the method of least squares would show

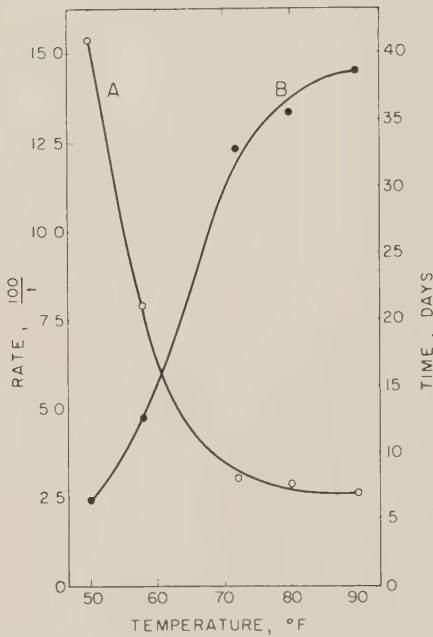


Fig. 19. Larval development through time of 50 per cent of those pupating at different temperatures. A, time-temperature curve; B, rate-temperature curve.

a theoretical zero point of 41.2° F, but experimental evidence is lacking to substantiate this threshold.

Puparium

Development in Relation to Temperature and Humidity. Puparia have been found in the field throughout the year and thus are subject to a wide range of temperatures. Laboratory studies have pointed out the importance of both temperature and humidity in influencing the rate and completion of development.

A study of development was made at seven constant temperatures that ranged from 43° to 100° F and with three different relative humidities at each temperature. Third instar larvae were examined every two to four hours while in their host plant. When a group of seven to 13 larvae had pupated prior to the last examination, they were removed for pupation tests. The transition from the larval to the pupal stage was not an abrupt process, so an arbitrary criterion of no movement after gentle contact was designated as the commencement of pupation. The leaves that enclosed the puparia were trimmed to a minimum and the group was placed in a 1,000 ml constant humidity flask (fig. 16) at the desired temperature. Examination for adults was made every two to four hours.

The results in table 7 show that completion of pupal development through emergence at temperatures ranging from 50° to 90° F, depended upon relative humidities. Varying numbers of adults formed within the puparia at all temperatures and humidities tried except in 59 per cent relative humidity at 50° F. An additional test was made at 100° F with 10 puparia in 45, 76,

TABLE 7
PUPAL DEVELOPMENT IN RELATION TO TEMPERATURE AND HUMIDITY

Temp. ° F	R.H. Per cent	Sat. deficit mm Hg.	Number puparia	Length of pupal stage, in days			Per cent adults formed	Per cent emerged	Expo- sure*
				Minimum	Maximum	Mean			
90 ± 1.....	{ 97 76 48	{ 1.1 8.7 18.8	{ 10 10 7	{ 4.5	{ 5.1	{ 5.0	{ 90 70 57	{ 90 0 0	{ 6 (44+) (94+)
80 ± 1.....	{ 98 76 51	{ 0.5 6.3 12.9	{ 10 10 10	{ 5.6 6.2 ...	{ 7.0 7.2 ...	{ 6.1 6.9 ...	{ 100 80 50	{ 90 60 0	{ 3 44 (89+)
72 ± 2.....	{ 98 76 54	{ 0.4 4.8 9.2	{ 13 11 12	{ 6.5 6.8 8.2	{ 7.8 8.7 8.5	{ 7.0 7.8 8.3	{ 92 82 33	{ 83 36 17	{ 3 37 76
58 ± 2.....	{ 98 77 56	{ 0.3 2.8 5.4	{ 9 9 9	{ 16.3 17.4 ...	{ 18.7 19.0 ...	{ 18.0 18.2 ...	{ 100 67 11	{ 100 33 0	{ 5 51 (98+)
50 ± 1.....	{ 98 77 59	{ 0.2 2.1 3.8	{ 8 8 8	{ 31.2	{ 36.3	{ 33.8	{ 100 25 0	{ 100 0 0	{ 7 (71+) (128+)

* Exposure is designated as the product of the mean pupal period and the saturation deficit. Parentheses indicate the use of the mean length of pupal stage of the next highest sample at which emergence occurred.

and 97 per cent relative humidities, but no adults were formed. Twelve adults formed at 43° F in a 98 per cent relative humidity, but no emergence took place and an examination after 90 days showed all to be dead.

The emergence percentages given in table 7 are based on the total sample and not upon the number of adults that formed. A marked decrease in the number of adults that formed and emerged was noted at each temperature as the humidity decreased. The length of time at which the puparia were exposed to the various saturation deficits becomes quite important when interpreting the resultant mortality. This relationship becomes more evident by comparing the figures in the exposure column, a comparison previously discussed under egg development. A larger sample with a more complete range of saturation deficits would be necessary to establish a definite exposure threshold.

As the moisture decreased, the pupal period was slightly increased at all temperatures (table 7) except when complete mortality prevented a comparison.

Limited observations indicate the pupal stage is somewhat resistant to low temperatures. Exposure of newly formed puparia at 28° F for five days resulted in only 50 per cent emergence after they were removed to 72° F for completion of development. No emergence occurred after 10 days exposure at 28° F.

Mean development times through emergence were taken from table 7 and plotted against their respective temperatures at 98 per cent relative humidity.

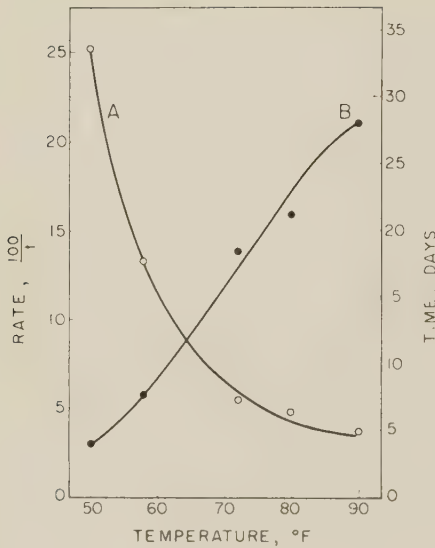


Fig. 20. Pupal development through mean time of emergence at different temperatures and a relative humidity of 98 per cent. A, time-temperature curve; B, rate-temperature curve.

to give the time-temperature or growth curve, A, in figure 20. The rate of development or rate-temperature curve, B, is also given, which is expressed at $100/t$ (t = time required for development through emergence). The rate of development curve expressed as a straight line by the method of least squares would show a theoretical zero point of 43.2° F. Experimental results showed imago formation at 43° F, but no emergence.

Table 8 gives a summary of development of the egg, larval, and pupal stages based on the result of tables 5, 6, and 7. These development periods compare favorably to most of those found by Kuwayama *et al.* (1955) for *H. griseola* at similar temperatures. Their investigations report the (calculated) critical low temperature for the egg stage at 50.2° F, larval stage at 42.8° F, and pupal stage at 46.4° F. These temperatures are within 1.6° to 3.2° F of the theoretical threshold temperatures determined in this work

TABLE 8
SUMMARY OF DEVELOPMENT OF IMMATURE STAGES AT
SELECTED TEMPERATURES*

Temperature ° F	Mean development period, in days			
	Egg	Larva†	Pupa	Total
90 ± 1.....	1.9	6.9	5.0	12.8
80 ± 1.....	2.3	7.6	6.1	16.0
72 ± 2.....	2.9	8.1	7.0	18.0
58 ± 2.....	7.5	21.1	18.0	46.6
50 ± 1.....	17.8	41.1	33.8	92.7

* Taken from tables 5, 6, and 7.

† Larval stage based on time that 50 per cent completed development.

for the larval and pupal stages, but are 6.3° F higher than the calculated threshold for the egg stage. Experimental evidence shows a lower threshold, as egg development was completed at a constant 43° F. A complete life history could not be consummated at a constant temperature of 43° F as pupae failed to emerge at this temperature. These investigations do indicate that the life history can be completed under a constant temperature of 50° F.

SEASONAL HISTORY AND FIELD ECOLOGY

The extensive distribution of *Hydrellia griseola* throughout California, both vertically and horizontally subjects it to a wide range of physical conditions. The seasonal history of the species would necessarily be expected to vary with temperature, moisture, soil type, and prevailing winds as they act upon the organism directly or indirectly through its host plants and habitat. The present study of *H. griseola* was concentrated in the Sacramento Valley and mainly in the vicinity of Davis. Limited observations were also made in the Coast Range foothills near Winters.

This section on seasonal history and field ecology is introduced with a presentation of the methods used in the study of population trends, including means of trapping the adults, the use of egg deposition plants, and the choice of meteorological equipment used in conjunction with the population indicators. Data obtained from these methods immediately follow the introductory sections, and for ease of reference are presented in chart form and as a separate unit.

The results from trapping and egg deposition, the influence of various physical and biotic factors, and general field observations are then discussed on a yearly basis in units of four overlapping months. These units begin with January and are divided in this manner in order to parallel major habitat changes due to seasonal sequence and the agricultural practices of man.

Methods Used for Study

Adult Trapping Equipment. The population of a species is composed of all the stages of its life cycle and for this reason the trapping or collecting of a single stage may not give a true indication of the abundance of the species. *H. griseola*, however, is a multivoltine species and all stages of its life cycle have been found throughout the year in varying numbers. The trapping of adults was one method used to give an index of the population. The collection of larvae and pupae would necessitate removal of part of the habitat, which at certain times of the year (when available host plants were scarce) seemed more detrimental than removal of adults.

The fly's habit of remaining close to the water surface and the absence of a yearly uniform habitat in which to sweep made it impractical to use the standard method of sweeping with a net. Several funnel-type traps with a bait at the base and inside the funnel were tried, but met with little success.

An open floating type of trap was eventually selected because the flies were most commonly found on the water surface, actively moving about in search of food, oviposition sites, and mates. The trap (fig. 21) consisted of



Fig. 21. Floating pan trap for adults.



Fig. 22. Floating pan trap with plexiglass rain shade.

an aluminum pan 8 inches in diameter and $1\frac{1}{4}$ inches deep, which was set in a circular hole cut in a 12-inch square of wood, $1\frac{1}{2}$ inches thick. The pan was attached to the wooden float by three screws through its $\frac{1}{2}$ -inch metal rim. A depression $2\frac{1}{2}$ inches in diameter and approximately $\frac{1}{2}$ -inch deep was hammered in the bottom of the pan to centrally locate the trapped insects. The trap was held in a horizontal plane by vertically placing $\frac{1}{4}$ -inch doweling through two eyelet screws on opposite corners of the trap and then forcing the doweling into the mud below. The eyelet screws were larger in diameter than the doweling, thus permitting vertical trap movement with water-level changes.

The pan was filled to within $\frac{1}{4}$ inch of the top with water and one to two milliliters of a wetting agent were added. "Tergitol 7" was the wetting agent primarily used although several others were tried and found to be satisfactory. The wetting agent reduced the surface tension so that an insect alighting on the water would become trapped by being wetted and eventually sink to the bottom of the pan. Contents of the traps were removed every one to three days with a glass suction tube. The contents of the suction tube were then passed through a second glass tube 1 inch in diameter that contained a 40-mesh brass wire cloth filter, so that the insects remained on the filter and the water containing the wetting agent passed back in the trap. The filter tube was then inverted and the insects washed into a vial of alcohol for future examinations.

A roof-shaped shield (fig. 22), made from fiber-reinforced plexiglass and attached to $\frac{1}{4}$ -inch hardware cloth, was placed on the two pieces of dowel extending above the trap during the months of heavy rainfall.

The advantages of the floating type of trap used in this study were as follows: (1) it could be located where adults were concentrated and most active; (2) a constant level of effectiveness was maintained in contrast to bait-type traps which may vary in degree of attractiveness; (3) the trapping

of the adults was dependent only on the activity of the fly, making it impartial in its selection in contrast to sweeping; and, (4) the size and simplicity allowed it to be made cheaply and it was easily changed to a new location.

Like most traps, there were disadvantages that must also be considered. The floating trap sometimes tipped and its contents were lost either through wave action from strong winds, or occasionally by both domesticated or wild animals. This was counteracted by placement of the traps in leeward locations or erecting an obstruction to break the wave action. The loss of records from one trap was compensated for by using a series of traps and only using the records from a constant number below the original series. Another disadvantage was that the collection of specimens in water necessitated preservation in liquid which in certain kinds of insect resulted in the loss of some systematic characters of differentiation. Liquid preservation, however, did not interfere with the identification of *Hydrellia*. It was necessary to collect the water-trapped insects at least every three days as they would tend to decompose, especially during periods of high temperatures. Finally, the trap was not selective and many species were caught in addition to the one being studied. This involved considerable time in sorting, but had the advantage of making it possible to record related species and adult parasites.

As is the case with most traps, the catch is dependent upon activity which in turn is limited by the weather. During the winter, when temperatures are below the minimum for activity of a species, trapping records do not necessarily give an indication of the species' true population. For this reason, the value of trapping records taken during this period lies in showing the presence and not the intensity of insect populations. The absence of a species in traps does not necessarily mean the absence of the species in the selected area.

It was not always possible to place each trap in an exact uniform location, but they were always placed 4 to 12 inches from the water's edge and usually next to grasses bordering the water. Traps were always at least 20 feet apart.

Egg-Deposition Methods. Egg-deposition information was obtained to supplement the trapping of adults. Potted barley plants, 5- to 10-weeks old, were placed in the field near the floating pan traps. These plants were arranged on a horizontal plane so that as many blades as possible were lying on the water surface. The leaves remained floating if the water level remained about the same. The plants were replaced every three days and egg counts were made in the laboratory with a binocular microscope. It was necessary to replant every three days so that barley plants of approximately the same size and age were continuously available. Five barley plants were grown in a single 4-inch pot and four of these pots were used simultaneously at different field locations. Barley plants were selected because they grew rapidly and were readily accepted for oviposition by the flies.

It was not possible to have the same number of blades in each pot or to arrange them on the water surface so they would be equally susceptible for egg deposition. Therefore, each pot was considered a plant unit and only the leaf blades which had eggs on them were counted. The total number of eggs per pot (plant unit) was then divided by the number of leaf blades

with eggs, to give an index of the mean number of eggs per egg-blade for that specific area. The indexes for the four plant units (pots) were then averaged to represent egg deposition in the general locality studied for that three-day period. The information was presented in six-day intervals (fig. 24), so the averages for the three-day periods were added and divided by two. This procedure may seem rather complex, but it was necessary not only because of the variation in the plants that were grown throughout the year, but also because of the placement of plants in a constantly changing environment which continually altered the plant-water surface relationship. The final units represent the number of eggs one would expect to find on a leaf blade that was susceptible to oviposition at various times of the year. The egg-deposition records follow the adult trapping records rather closely, which is to be expected as oviposition is an important part of adult activity throughout the year.

Choice of Meteorological Equipment

The physical environment must be considered in any insect biological or ecological study, particularly when searching for reasons for abundance, distribution, and behavior. The problem soon arises of what type of instruments to use and where to place them to provide information that can be interpreted and related to biological observations. Very often the subject being studied occupies a microenvironment or "insect climate" that is quite variable and requires highly specialized recording equipment. Such was the case with the various stages of *H. griseola*. The eggs are laid on the outside of leaves and are subject to certain environmental changes such as transpiration of the leaf. In addition, the leaves are usually located close to the water at distances varying from 0 to 6 inches. The larvae and pupae are confined in the leaf blades in a special environment that is generally quite moist and often much warmer than the surrounding air during the day and cooler at night. The adults are very active and are found in a great variety of situations depending on the time of year, but are most commonly observed within a 12-inch zone over the water.

The microclimate, however, is indirectly controlled by the macroclimate even though the two environments may not always directly parallel each other. Meteorological equipment used to measure the macroclimate is more readily available and can be operated by a single individual when limited to a few instruments. Information obtained from this type of equipment has been used widely by entomologists to study distribution and abundance of a species with varying degrees of success. It is the author's opinion that one of the greatest uses of such information, when taken concurrently with a record of species abundance, is to point out the climatic or phenological periods of several years that appear to be most critical for the species. When these critical periods are known, a concentrated study may be made of the microenvironment to possibly determine actual limiting physical factors.

The meteorological equipment used for this study varied somewhat during the three-year study period because of availability and attempts to adapt the instruments most suitably to the habitat. Most of the data obtained represent a compromise between what the insect is experiencing and the stand-

ard instrument shelter or "human climate." This compromise falls in what might be called the plant zone or "plant climate."

Water temperatures were continuously recorded just beneath the water surface. In 1954 the capillary bulb of a Foxboro recorder was extended to a wooden float so that the bulb was 1 to 2 inches below the surface. A shield was attached to the float in order to shade the bulb. Wind action against the shield tended to tip the float excessively. In 1955 the capillary bulb of an Auto-lite thermograph was fixed to a wooden dowel extending vertically in the water. The unshaded recording bulb varied from $\frac{1}{2}$ to $1\frac{1}{2}$ inches below the water surface. The fixed arrangement required considerably more attention as water level fluctuated. In the latter part of 1955 and 1956 the bulb was again attached to a wooden float, but without a sun shield. This gave an unshaded water temperature approximately $\frac{1}{2}$ to $1\frac{1}{2}$ inches below the surface and proved to be the most satisfactory arrangement. Recordings are presented in figures 23 and 26.

Shaded air temperatures were continuously taken with a Friez hydro-thermograph located in a ventilated shelter. In 1954 the shelter was set 7 to 8 inches above the levee within a rice field. The shelter was placed directly on the ground during 1955 and 1956, either on a rice levee or the edge of several ponds that were studied. The temperature recordings are presented in figures 23 and 25.

"True air temperature" is strived for by protecting the sensitive element from radiation and providing forced ventilation. This type of temperature is probably the most commonly used in meteorological work. Those interested in biological processes, however, desire a temperature that is more indicative of what the object of their studies is experiencing. An instrument of this type must show combined response to radiation, convection, et cetera, and be located at the same exposure as the organism being studied. Various test objects have been used to record this type of temperature and they fall under the general classification of experimental bodies. Their temperatures are subject to the same kind of radiation and wind, even if they are not subject to the same amounts as the plants or animals themselves. The type of experimental body used to obtain radiation temperatures during 1955 and 1956 was a thermograph capillary bulb 7 inches long and $\frac{5}{16}$ -inch in diameter. It was painted flat black and placed horizontally, $\frac{1}{2}$ to $1\frac{1}{2}$ inches above the water surface. In 1955 its position was fixed on the same vertical doweling as the water-temperature bulb and in 1956 it was attached to the wooden float opposite the water-temperature bulb. Radiation temperatures are given in figures 25 and 27.

Records of rainfall were taken from the weather station at Davis, which was 3 miles southwest of the area being studied. The amount and frequency of precipitation at the study area were undoubtedly not the same, but close enough to be indicative of the effect of rain upon the growth of vegetation and formation of rain pools. Rainfall for 1955 and 1956 is presented in figure 26.

Two black Livingston atmometers (No. 5D c.f. 0.78) were employed at separate levels during the 1954 and 1955 rice seasons. One was located approximately 2 inches above the water surface (attached to the float, or fixed

TABLE 9
EVAPORATION FROM BLACK LIVINGSTON ATMOMETERS AT SEPARATE
LEVELS IN RICE FIELDS OF 1954 AND 1955

1954	Total evaporation in ml of water			1955	Total evaporation in ml of water		
	(A) Over water*	(B) Over levee†	(B) (A)		(A) Over water*	(B) Over levee†	(B) (A)
May 16.....	326	424	1.3	May 13.....	279	364	1.3
22.....	375	525	1.4	19.....	456	577	1.3
28.....	413	574	1.4	25.....	486	664	1.4
June 3.....	427	624	1.5	31.....	424	568	1.3
9.....	319	432	1.4	June 6.....	500	665	1.3
15.....	324	478	1.5	12.....	390	553	1.4
21.....	544	686	1.3	18.....	304	414	1.4
27.....	362	527	1.5	24.....	401	557	1.4
July 3.....	316	524	1.6	30.....	359	486	1.4
9.....	264	735	2.8	July 6.....	324	490	1.5
15.....	214	404	1.9	12.....	322	512	1.6
21.....	215	435	2.0	18.....	305	496	1.6
27.....	235	490	2.1	24.....	300	475	1.6
Aug. 2.....	110	292	2.7	30.....	217	378	1.7
8.....	110	320	2.9	Aug. 5.....	245	489	2.0
14.....	74	286	3.9	11.....	182	407	2.2
20.....	91	283	3.1	17.....	160	370	2.3
26.....	80	222	2.8	23.....	129	349	2.7
Sept. 1.....	78	249	3.2	29.....	120	326	2.7
7.....	71	233	3.3	Sept. 4.....	126	324	2.6
13.....	69	225	3.3	10.....	87	259	3.0
19.....	79	202	2.6	16.....	81	248	3.0
25.....	72	232	3.2	22.....	78	206	2.6

* The base of the black bulb was approximately 2" above water.

† The black bulb was approximately 22" above the levee and 40" higher than the water.

‡ The black bulb was approximately 30" above the levee and 40" higher than the water.

stand) and the second was placed over the levee so that it was approximately 40 inches higher than the water level. The Livingston atmometer (Briggs and Shantz, 1917) has been used to indicate the evapotranspiration potential and is an instrument combining response to radiation, wind, and humidity. Six-day totals of milliliters evaporated from the instruments are given in table 9. The instruments were not moved during the summer and therefore received more shade toward the latter part of the season as vegetation increased in height. Wave action occasionally caused the base of the lowest bulb to touch the water so the readings of this atmometer may be slightly low. No direct correlation with leaf miner abundance was found by their use, but they provide supplementary information which was descriptive of the rice field as a habitat.

Seasonal Abundance in Relation to Weather

The information presented in this section was obtained through field studies near Davis during the rice season of 1954, continuously from January of 1955 to July of 1956, and at a small artificially maintained pond at Davis from October of 1955 to July of 1956.

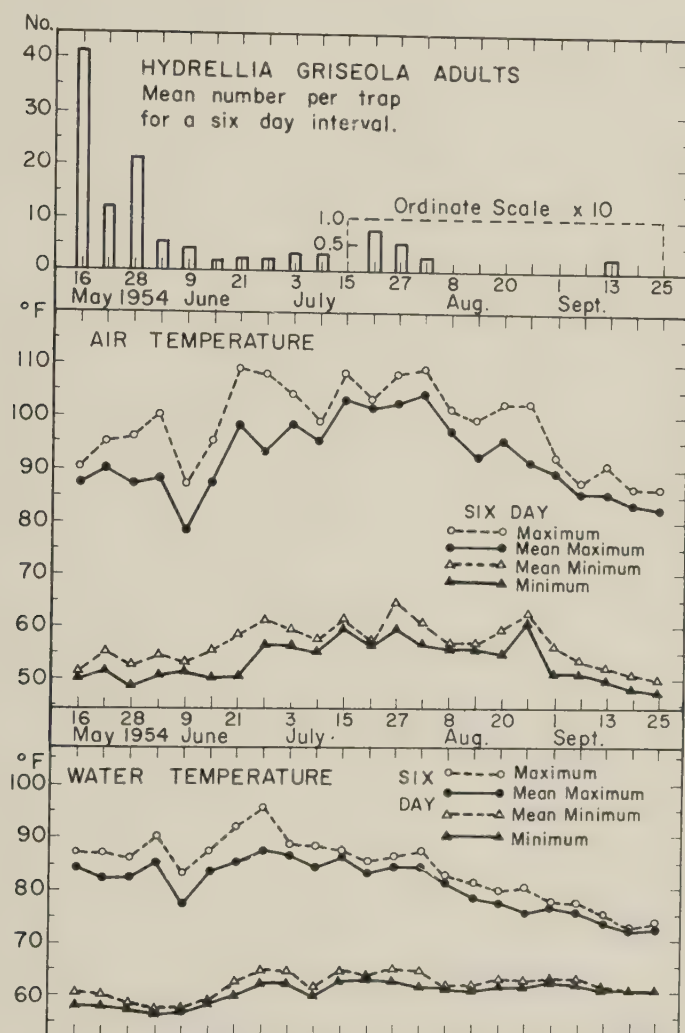


Fig. 23. Adult trapping records, air and water temperatures at a rice field 6 miles NE of Davis, in 1954. This field was planted to rice for the second consecutive year.

Explanation of figure:

Adult trapping record. Based on mean number of adults per trap from a sample of four traps. Traps were located in the same rice check as the temperature recording equipment, but distributed along the rice levee approximately 40 yards on each side of the equipment.

Air temperature. Taken with a shaded hygrothermograph, 7 inches above the rice levee.

Water temperature. Taken 1 to 2 inches below water surface from a shaded float on water varying in depth from 4 to 12 inches. The source of the water was from a single well and supplemented by canal water, but the recordings were taken in the sixth check below the water source.

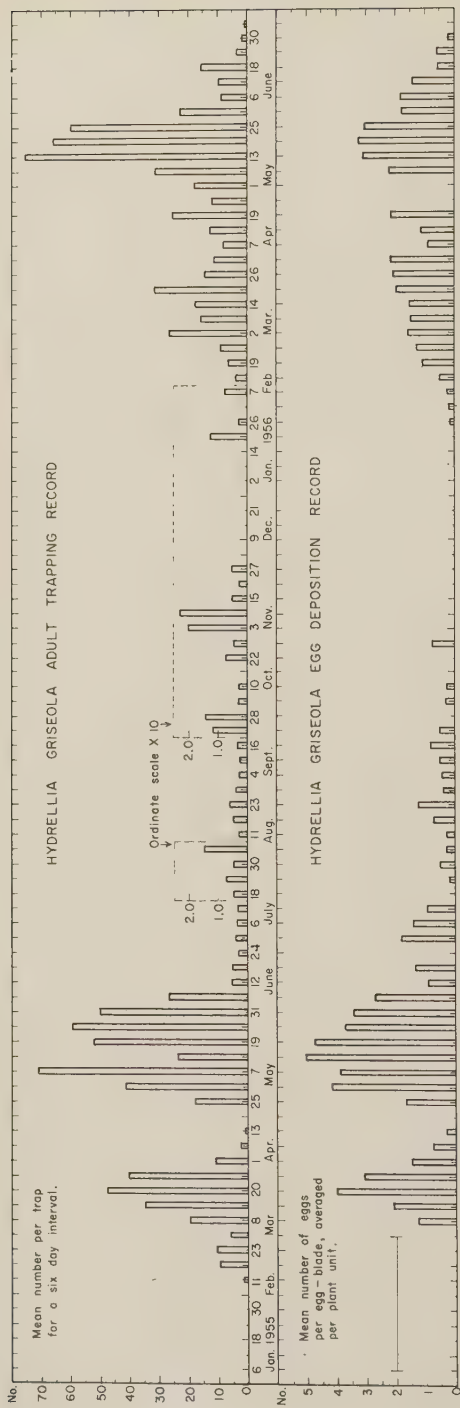


Fig. 24. Adult trapping and egg deposition records in association with rice fields approximately 3 miles NE of Davis, in 1955 and 1956.

Explanation of figure:

1955 January 1 to April 25. Low drainage areas and ditches bordering the rice field and receiving water from natural rains.

April 25 to September 22. Rice field and its irrigation network which was planted for second consecutive year.

September 22 to January 8. A linear-shaped pond approximately 105 square feet and varying in depth from 4 to 12 inches, which was located at the inlet of the same rice field. Water level was maintained by the intermittent addition of well water and by normal rainfall.

1956 January 8 to May 1. Low drainage areas and ditches between the 1955 and 1956 rice fields. The areas received water from natural rains. May 1 to July 6. A rice field and its irrigation network $\frac{1}{4}$ mile south of the 1955 field. This field was planted in rice for the first time.

Adult trapping record. This was based on mean number of adults per trap, of the four highest of six traps, situated in the areas listed above.

Egg deposition record. Every three days, four pots of barley plants were placed on the water surface in close association with the adult traps. Two three-day periods were averaged to give the mean number of eggs per blade with eggs, which were then averaged per plant unit.

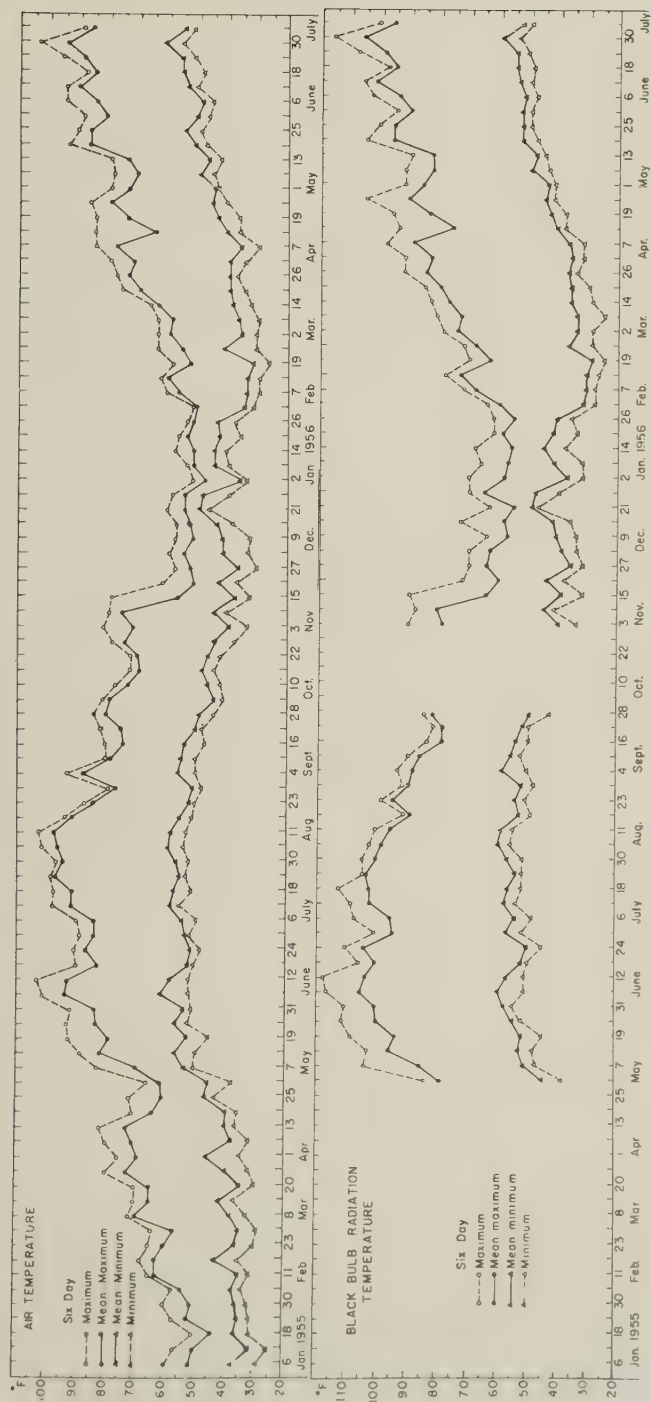


Fig. 25. Air and radiation temperatures at the location of the 1955-1956 traps.

Explanation of figure:

Air temperature. Records from a hygrothermograph were taken at 3 to 4 inches off the ground in a shelter located on the levee adjacent to the trapping studies, with the exception of those from January 1 to March 2, 1955, which were taken at the Davis Weather Station. Specific localities throughout 1955 and 1956 are the same as reported in the explanation of figure 24. The temperatures are reported in six-day intervals to correspond with trap collections and oviposition counts of figure 24.

Radiation temperature. A continuous recording temperature bulb, 7 inches long and $\frac{3}{16}$ inch in diameter was painted flat black and placed 1 $\frac{1}{2}$ to 1 $\frac{3}{4}$ inches above the water surface. It was located in the areas of trapping studies which are specified in the explanation of figure 24.

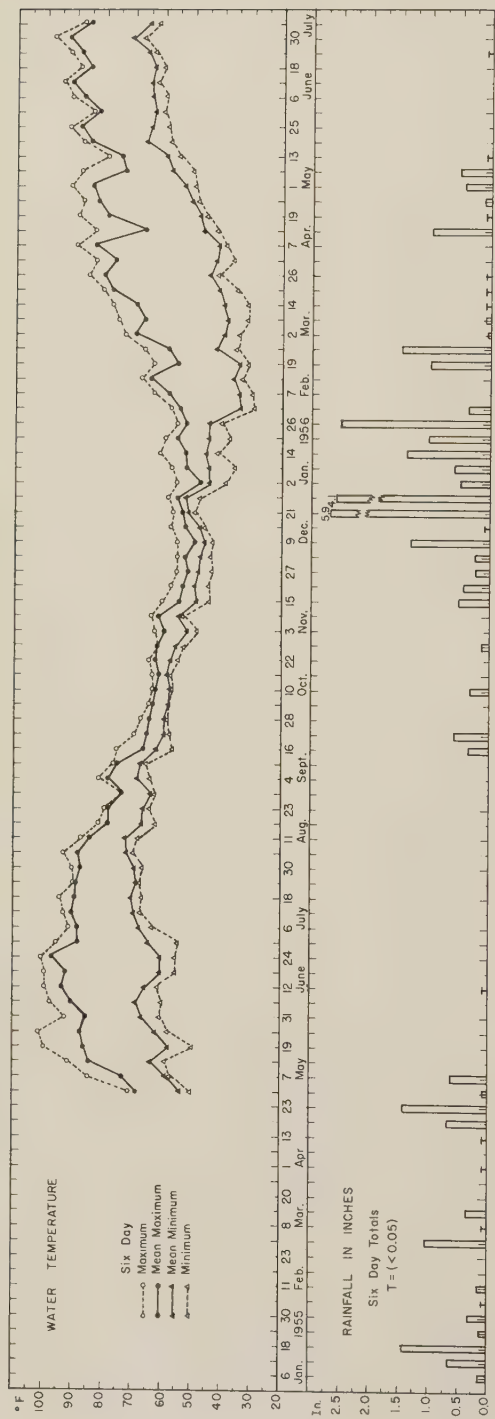


Fig. 26. Water temperature at the location of the 1955-1956 traps and rainfall at Davis.

Explanation of figure:

Water temperature. A continuous recording from an unshaded liquid temperature bulb, $\frac{1}{2}$ to $1\frac{1}{2}$ inches below the water surface, was taken in the area of trapping and oviposition studies. Specific localities and source of water throughout 1955 and 1956 are the same as reported in the explanation of figure 24. The drainage areas studied between January 8 and May 1, 1956, consisted of small ponds of approximately 5 to 15 square feet in which the water was 4 to 5 inches in the deepest part. Changes to different ponds were made on March 14, 29, and April 23 within this drainage area because the water depth had dropped to 1 to 2 inches due to seasonal evaporation and drainage. Water depth of the 1955 and 1956 rice field study areas is given in figures 36 and 37. The rice fields received their water from wells in 1955 and 1956 but the recording equipment was located several cheeks below the inlet.

Rainfall. Measurements of rainfall were taken at the Davis Weather Station.

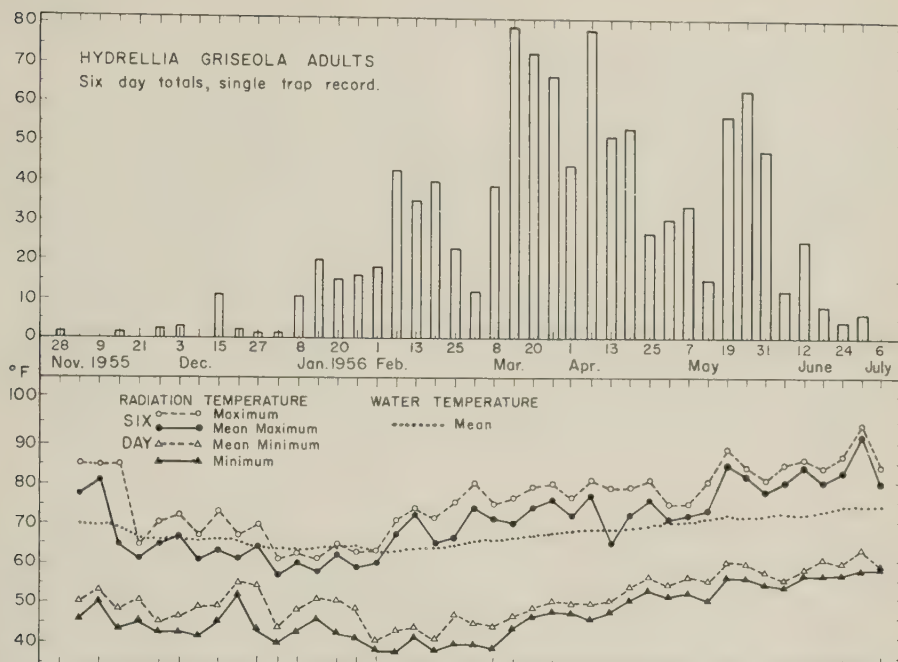


Fig. 27. Adult trapping record and weather data at an artificially maintained pond at Davis, 1955-1956.

Explanation of figure:

Location. A small pond, with a surface area of approximately 60 square feet and depth varying from 2 to 6 inches, was formed on the Davis campus October 12, 1955. It was artificially maintained with a continuous flow of well water, and ample host plants.

Adult trapping record. The records presented are based on the six-day totals of a single trap.

Radiation temperature. A continuous recording temperature bulb, 7 inches long and $\frac{7}{16}$ inch in diameter, was painted flat black and placed 1 inch above the water surface.

Water temperature. A continuous recording from an unshaded liquid temperature bulb, $\frac{1}{2}$ inch below the water surface, was taken under the radiation bulb where the water was 4 inches deep. Only the mean temperature is presented, as the maximum and minimum were never more than 2° to 3° F apart during the six-day intervals which are plotted.

More specific information relative to trapping and oviposition methods, and choice of meteorological equipment has been reported in the three previous sections. A discussion of species abundance in relation to the weather and habitat changes will be presented in the following sections under the respective seasons.

At least one trap and oviposition plant were always placed in close association with the meteorological equipment. The other traps and plants were distributed in selected situations in the same general habitat. At times, however, conditions in the area varied from the specific situation where the

instruments were located. This condition was especially true during the summer of 1955 and is discussed further in the section on survival in limited areas.

Initial Buildup on Wild Grasses, January to April

Type of Habitat. December and January are the months of highest rainfall (table 10) and usually by the end of January the fields of the Sacramento Valley are amply covered with standing rain pools (figs. 28 to 31).

TABLE 10

DEVIATIONS FROM CLIMATOLOGICAL DATA AT DAVIS, 1953 THROUGH 1956

Period	Mean temperature	Days maximum temperature 60° F or above	Days minimum temperature below 30° F	Rainfall	Evaporation
	° F			in	in
January					
Average.....	44.5*	7.5†	7.0‡	3.52‡	1.18§
1953.....	+6.5	+4.5	-7.0	-0.66	-0.15
1954.....	+2.6	-1.5	-7.0	-0.29	+0.14
1955.....	-1.9	-6.5	-4.0	-0.84	+0.08
1956.....	+3.3	-6.5	-7.0	+2.57	-0.53
February					
Average.....	49.5	15.0	2.5	2.98	1.90
1953.....	+1.6	+9.0	-1.5	-2.95	+1.46
1954.....	-0.6	-7.0	-2.5	+0.56	-0.27
1955.....	-1.1	+2.0	-1.5	-1.76	+1.04
1956.....	-3.5	-5.0	-1.5	-0.41	+0.71
March					
Average.....	53.5	25.5	0.5	2.36	3.68
1953.....	-0.4	-2.5	-0.5	-0.50	+0.35
1954.....	-2.9	-6.5	-0.5	+0.15	+0.38
1955.....	+0.6	+1.5	-0.5	-1.96	+1.91
1956.....	+0.5	+1.5	-0.5	-2.28	+1.51

* 40-year average.

† 80-year average.

‡ 20-year average.

§ 27-year average.

These averages compiled by H. B. Shultz at the Davis Weather Station.

The duration of these pools depends upon many factors, such as frequency and amount of rainfall, evaporation rate, topography, and soil type. The heavy clay series of soils—most desirable in rice culture for their water retention properties—also prolong the longevity of standing rain pools.

The grasses present at this time are an accumulation of those continuing from late summer and early fall irrigation practices, and new growth starting with the advent of fall and early winter rains. *Lolium*, *Avena*, *Polygonum*, *Oryza* (voluntary), and *Hordeum* are the most commonly found genera of grasses. The relationship of these grasses to the standing rain pools is important in establishing breeding situations for *H. griseola*. Areas that have been continuously submerged during the summer, such as rice field checks and canals, have very little new growth except on their banks. The areas bordering rice fields and roadway ditches, however, are usually abundantly covered with new grasses, and their collection of winter rain

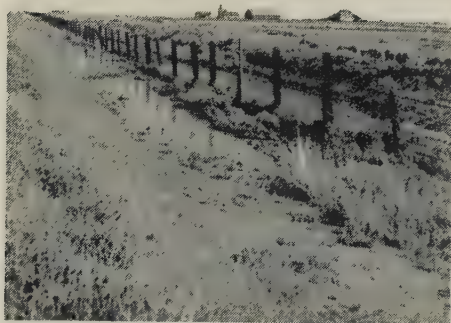


Fig. 28. Rain pool between road and rice field (March, 1955).

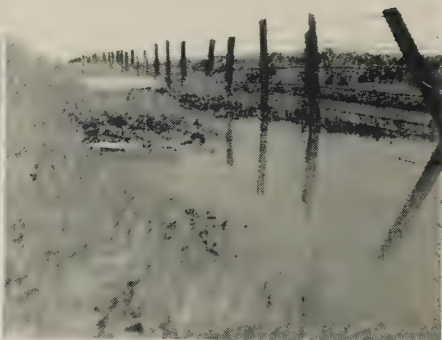


Fig. 29. Close-up of area of figure 28, showing trap site and oviposition plant.

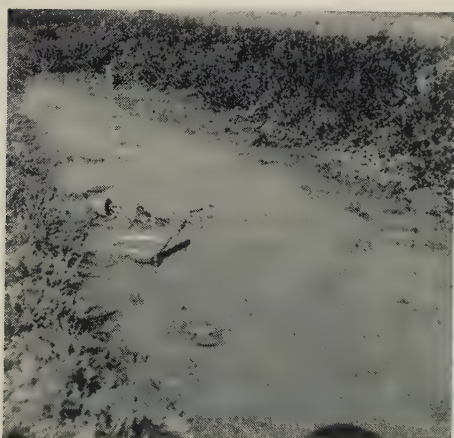


Fig. 30. Rain pool bordering a rice field in mid-March of 1955.



Fig. 31. The same pool as figure 30 by the end of March.

provides an excellent situation for oviposition and mining. In limited areas that received seepage from late summer irrigation, grasses were in an advanced stage of growth. Water from winter rains collect in these areas with the result that much of the vegetation emerges from the water and also borders the newly formed pools.

The water level of the pools fluctuates proportionately with the frequency and the amount of rainfall. Grass growth increases as the weather becomes warmer, but its relationship to the water level of the rain pools becomes more distant as the pools lose water by evaporation and seepage (figs. 29 to 31). An exception to this occurs in those pools with emergent grasses.

The increased flow of water in streams and rivers during these months also provides a favorable habitat for *H. griscola* as the water level often

reaches the grass-covered banks and water occasionally overflows to form temporary pools.

The First Generation. Field observations in the vicinity of Davis during the month of January (1954 to 1957) consistently revealed adults, but the observed numbers of flies during this month was low. The probability of finding flies in January in any specific area depended on several factors: (1) a temperature sufficiently high to permit activity (above 50° F); (2) a suitable grass-water relationship, favoring concentration of the flies; and (3) the proximity of the observed area to those localities that supported late summer and fall generations.

Activity was not recorded in the 1955 adult traps until February 6, but the 1956 traps revealed flies as early as January 17. This three-week difference was probably due to the warm January temperatures of 1956, which were 5.2° F higher than the January mean of 1955 (table 10). Initial oviposition closely paralleled the first adult trap catches.

Figure 24 shows the general rise in the number of adults collected and the oviposition rate until the latter half of March. These rises are due in part to the longer days and higher temperatures which permit increased adult activity, and also to the additional movement of flies to the ponds containing the traps. The traps were located in situations with deeper and longer lasting rain pools. March of 1955 and 1956 each had less than 1/2 inch of rainfall which was more than 2 inches below normal. Consequently, the rain pools began drying up by the middle of March, and by the first of April very few pools remained. Figures 30 and 31 show the progressive drying of a pool. As the pools decreased in size, the adult trap and oviposition records decreased, as shown in figure 24. Oviposition ceased if the grasses were no longer in close proximity with the water and early instar larvae often failed to complete development. Pupation started during the latter half of March and emergence of the first generation began during the first half of April.

The Rice Field as a Habitat, April to July

Prevailing Climate. Table 11 presents some of the climatic averages of this period and deviations from these averages during the years *H. griseola* was studied. Adult trapping and oviposition records were not taken during the serious outbreak of the rice leaf miner in 1953 (Lange *et al.*), but it is interesting to note the weather conditions during this year when adult and larval activity was reported in great abundance. From January through May of 1953 (tables 10 and 11) the monthly mean temperature increased from 51.0° F to 60° F, whereas the average increase is from 44.5° F to 64.1° F. Unfortunately, this combination of a mild winter and cool spring was not repeated during the following years when trapping and oviposition studies were being conducted.

Agricultural Practices and the Second Generation. Most of the rice acreage in California is usually seeded between April 15 and May 10. Seeding after May 30 is not recommended because of crop losses from fall rains and immature stands. By the latter part of March, the decreased rainfall, warmer temperatures, and drying winds have usually dried the land suffi-

TABLE 11

DEVIATIONS FROM CLIMATOLOGICAL DATA AT DAVIS, 1953 THROUGH 1956

Period	Mean temperature	Days maximum temperature 90° F or above	Rainfall	Evaporation
	° F		in	in
April				
Average.....	58.3	1	1.21	5.70
1953.....	-0.8	-1	+1.04	-0.26
1954.....	+3.6	+1	+0.48	+0.30
1955.....	-4.3	-1	+0.96	+0.42
1956.....	+0.1	-1	+0.29	-0.09
May				
Average.....	64.1	6	0.64	8.25
1953.....	-4.1	-6	-0.29	-1.54
1954.....	+2.2	0	-0.48	+0.93
1955.....	+1.9	+2	0.00	+1.02
1956.....	+1.1	-1	-0.10	+0.17
June				
Average.....	71.0	14	0.19	9.80
1953.....	-2.9	-7	+0.28	-0.35
1954.....	-0.4	-3	-0.03	+0.83
1955.....	-1.0	-2	-0.19	+1.21
1956.....	+0.8	-2	-0.17	+0.54

ciently for cultivation to begin. Land which has not been previously planted to rice is thoroughly cultivated and is completely devoid of vegetation. A field planted to rice the previous year may also be cleanly cultivated by several methods, but generally the levees contain an abundant growth of new grasses.

While the land is being cultivated for seeding, irrigation water is brought into the area in preparation for flooding. This irrigation water creates many sites that are suitable for oviposition. Favorable new oviposition sites are again provided when the rice fields are flooded and the water level comes in contact with grasses on the levees.

During this period, the agricultural practices of man completely reverse the seasonal trends of nature. Irrigation creates numerous areas that favor the continued buildup of the rice leaf miner. This occurs when the spring habitat is drying up and the carry-over into the second generation normally would be dependent upon streams, rivers, and permanent ponds.

The trapping and oviposition records of 1955 (fig. 24) show little activity from April 7 to 19 at the rain pools which were completely or very nearly dry. Submergence of the rice field started April 20 and records from traps and oviposition plants within the field sharply increased. This sharp rise was not only due to the creation of a favorable habitat, but was also the result of an increased number of flies emerging from the first-generation pupae. The 1955 field contained an abundant growth of grasses on the levees (*Arena*, *Lolium*, *Phalaris*, and *Polypogon*) and oviposition began immediately. Flies of this second generation started to emerge from puparia after May 15.

The same general trend was observed in 1956. Trapping and oviposition records were decreasing as the pools were evaporating. The counts did not

fall as low during April of 1956 as the previous year, because some of the traps and plant units were relocated in areas containing irrigation water. The subpeak of April 19 (fig. 24) was probably due to the emergence of adults from the first generation, as puparia were observed as early as April 5. The lack of oviposition records and the decrease in adult counts of April 25 and May 1 are, in part, due to the loss of records, as several traps and plants that were located in the irrigation ditches were swamped because of sudden changes in water level. Flooding of the 1956 rice field was started April 28. The field was planted in rice for the first time which resulted in levees bare of vegetation. Traps located in the rice field checks yielded very few adults; however, canals and drainage ditches in close association with the rice field contained dense grass growth and traps and oviposition plants in these areas showed a steady increase in activity. Flies began emerging from puparia of this second generation about the middle of May.

The second generation of *H. griseola* (mining the grasses of rice levees and irrigation channels) was subject to some of the cooler temperatures of occasional spring storms, but in general there was a steady rise in daily maximums and minimums. This was reflected in a shorter development time (approximately 25 to 35 days), less than half the time taken by the first generation.

Development on Rice. The rice fields that were studied in 1954, 1955, and 1956, were seeded May 7, April 24, and May 1, respectively. Early growth of rice takes place while the plants are completely submerged, so water temperature becomes an important factor in the growth of the crop. An average depth of 5 to 7 inches is usually maintained at this time. Temperatures of water at this depth fluctuate with air temperatures, but loss and gain of heat by the water are slower than the rapid change of air temperatures, resulting in a modulation effect upon the environment. Night-time minimum water temperatures in a rice field are generally 5° to 10° F higher than air temperatures 1 to 2 feet above the water. Daytime maximum water temperatures may be higher or lower than shaded air temperatures depending on such factors as water depth, circulation, and the amount of shade a given area receives from emergent vegetation.

Rice field levees are usually built on a 0.2- to 0.3-foot elevation decrease of the land. Each area of land between levees would ideally be level, but a rice check that has an average 5-inch layer of water may have a variation of 1 to 10 inches in different areas of the check. The construction of levees usually creates deeper areas paralleling them, called "barrow pits," which may be as deep as 12 inches. The water depth is also occasionally altered by the variable irrigational practices of individual growers. It was a common practice for the growers in the area studied to reduce the flow of water and drop the level 16 to 20 days following seeding. The purpose of maintaining a 5- to 7-inch water layer at the first of the season is to prevent the germination and growth of watergrass (*Echinochloa crusgalli*). The water level is dropped after this period to bring the rice plants above the surface. The latest recommendations, however, are to maintain a constant water level and allow the rice plants to grow through the original water depth. Because of the fluctuation of water in those fields studied, recording

instruments were permanently located at the deeper part of a rice check and supplementary temperature readings were made in the shallow parts.

The water level was dropped below the height of the rice plants on approximately May 24, 1954, May 13, 1955, and May 16, 1956. The adult trapping records shown in figures 23 and 24 demonstrated that the greatest catches of the year occur just prior to or during the period of rice emergence. The largest segment of this adult population probably resulted from the first generation of the year, but the second generation is also emerging at this time and could contribute to the total catch. The oviposition records given in figure 24 also exhibit peak activity during these same periods.

The lowered water level almost invariably leaves the blades of the rice plants lying flat on the water surface and flies immediately begin ovipositing on them. Figures 36 and 37 show a rice check under study in 1955 at a time when the water was being lowered and the rice was lying flat. The extent and intensity of infestation of the rice plants by the immature stages of *H. griseola* in 1955 and 1956, are presented in figures 34 and 35. The information was obtained by the periodic examination of a random sample of 25 plants from an area in the rice check where the temperature recording instruments were located. The plant growth in relation to average water depth is also given in these figures. In 1954, the random samples were collected from several checks and not necessarily repeated in the same areas, but this sampling method proved unsatisfactory due to variations in degree of infestation.

The data presented in figures 34 and 35 show that the intensity of the infestation was greater in the selected rice check of 1955, than in 1956. Several reasons may be advanced to explain the observed differences between the two years. The 1955 check was in a second-year rice field which harbored an abundant growth of grass on its levees (fig. 32). These conditions favored



Fig. 32. Newly flooded second-year rice field in May, 1955. Note abundant grass growth on levees.



Fig. 33. A first-year rice field in June, 1956. Note levees bare of vegetation.

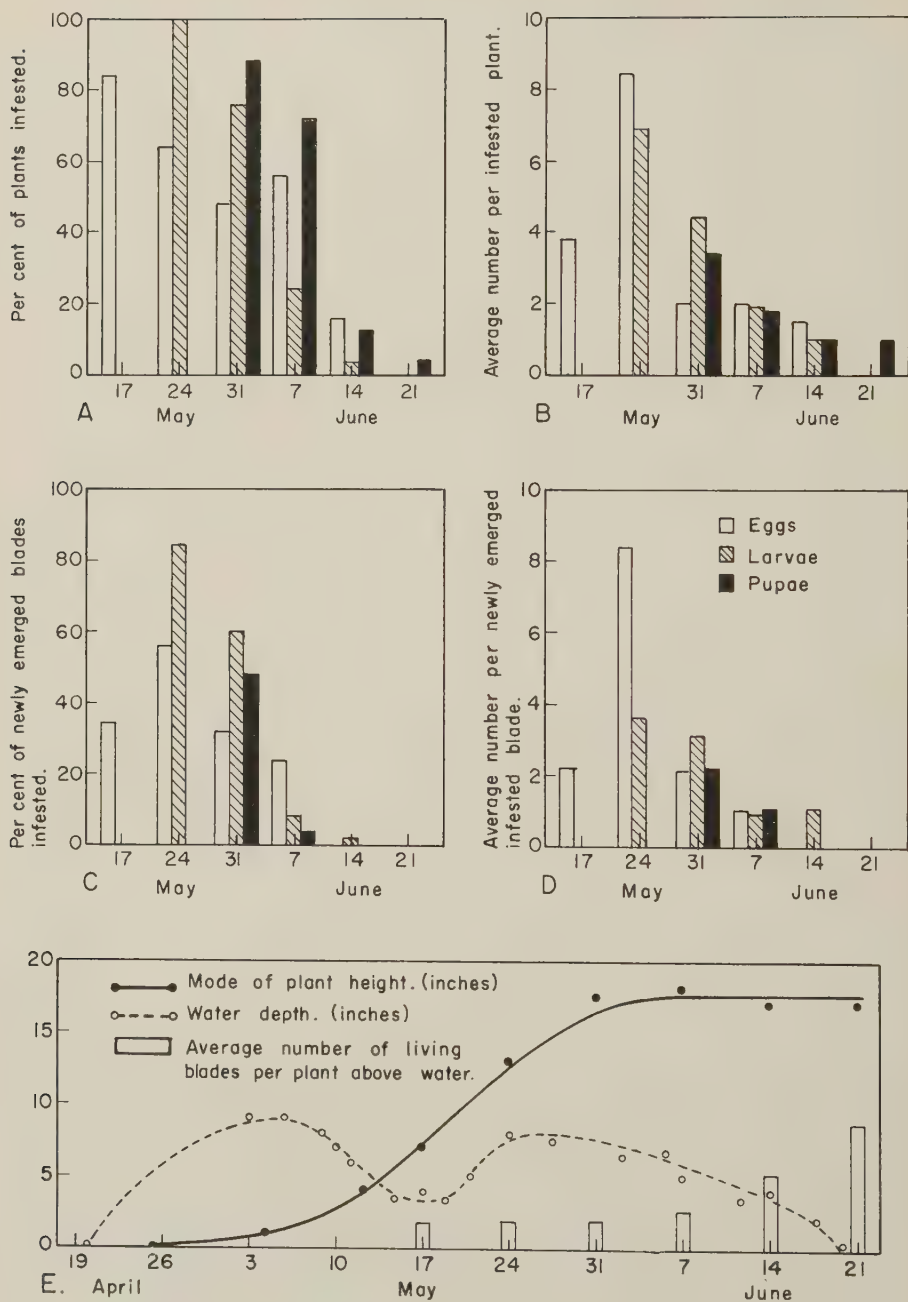


Fig. 34. Seasonal abundance of immature stages of *Hydrellia griseola* in a rice field at Davis, during 1955 in relation to certain ecological factors. A, B, C, and D: extent and intensity of stages; E: plant growth in relation to water depth.

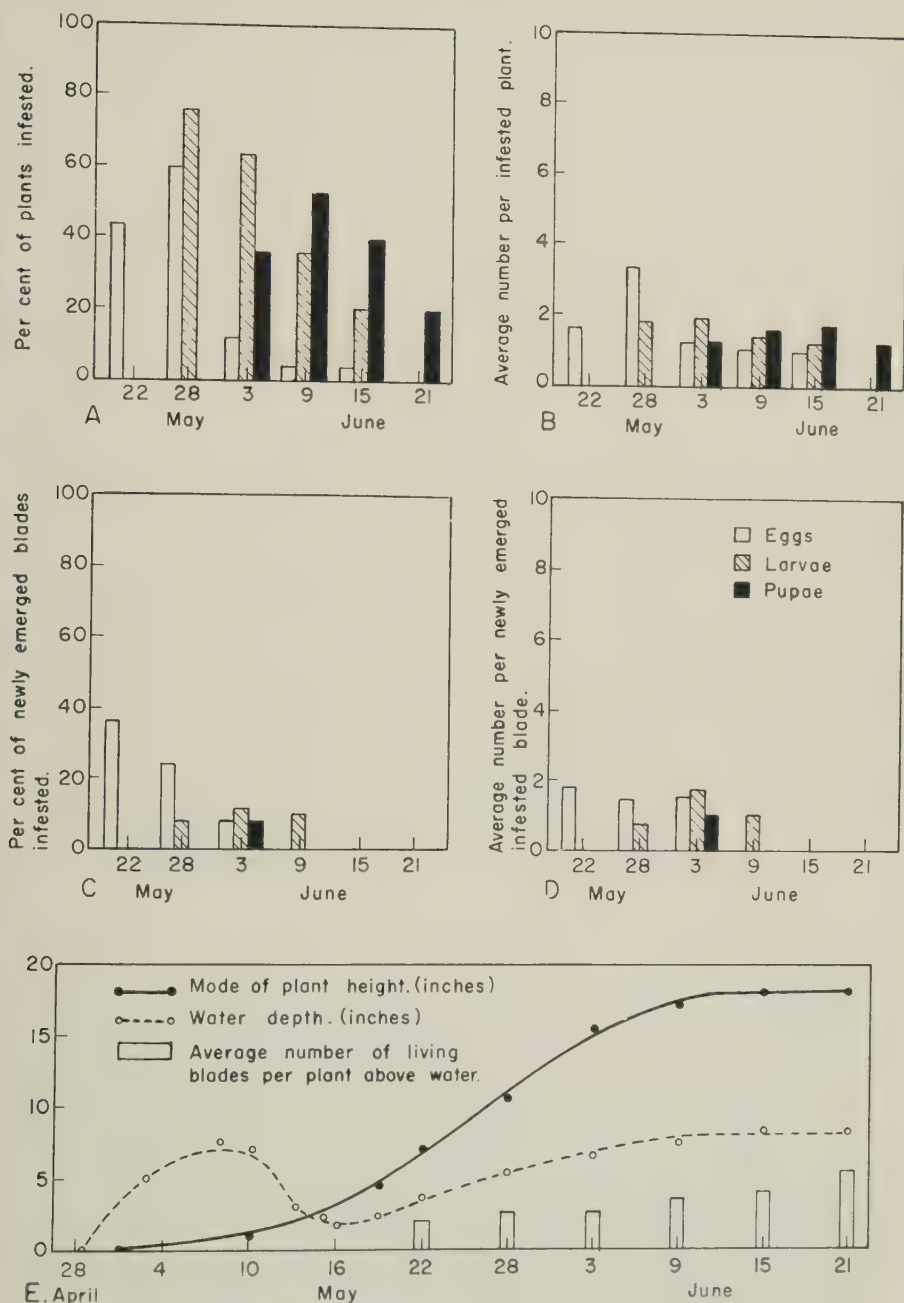


Fig. 35. Seasonal abundance of immature stages of *Hydrellia griseola* in a rice field at Davis during 1956 in relation to certain ecological factors. A, B, C, and D: extent and intensity of stages; E: plant growth in relation to water depth.

a high population of adults which were not only present, but also continued to emerge from the levee grasses at a time when the rice was lying on the water. The 1956 rice check on the other hand, was in a first-year field, with levees free of grasses (fig. 33). It was necessary for flies to move into the field from adjacent grassy irrigation and drainage ditches to infest the emerging rice. This theory is partially supported by the lower number of 1955 (figs. 34A and 35A), and also by a lower adult catch in 1956 in the rice plants infested with eggs at the first count in 1956 in comparison with traps located in the rice field proper. Another factor could have been the greater water depth of the 1955 rice check in comparison with the 1956 check. In addition, the water level in 1955 was raised too fast and many rice plants were again lying flat on the water surface, whereas in 1956 the water was slowly raised behind the plant growth which allowed them to remain upright.

Under favorable conditions, many of the rice blades will lift from the water surface and begin upright growth. New growth emerging through the water will nearly always remain upright, even if the older blades remain on the water surface. Figures 38 and 39 show the 1955 rice check on May 19. The water had been lowered for several days prior to this date and many of the rice plants had started upright growth, particularly in the shallower portions of the check.

The conditions that retard or prevent rice blades from attaining a vertical position and thus increase susceptibility to attack from the miner, are as follows: (1) unfertile soil and low temperatures result in weakened plants and slow growth; (2) heavy wind movement by direct force, wave action, or by forcing algal growth over floating rice blades; and (3) permanent excessive deep water or mismanagement of water by increasing its height too fast after the initial drop; (4) heavy algal growth (*Gloeotrichia* sp. appeared to be the most dominant type found in 1954 through 1956) will occasionally break lose from underwater substrata and form large floating



Fig. 36. Rice check on May 14, 1955, when water was being dropped. Note the rice lying on the surface.



Fig. 37. Close-up of a section in figure 36.

blankets. These floating patches often collect at the drainage end of a check or areas with poor circulation, where they stick to floating rice blades and prevent their rising and hinder new growth from breaking through.

These four factors are all detrimental to plant growth and favor continued activity of the rice leaf miner. The best measure of the seriousness of an attack by *H. griseola* on rice is the extent and intensity of activity on the newest plant growth. The first one or two rice blades that are above water may be mined without killing the plant if new growth is allowed to continue, although it undoubtedly weakens the plant and may delay maturity. If conditions are such that the new growth is continually mined, then the plant dies because of interruption of nutritional and respiratory functions.

Figures 34 and 35, parts C and D, show degree of infestation of the newest growth in 1955 and 1956. Mining activity on the new growth was higher



Fig. 38. Rice check on May 19, 1955, at low water level.

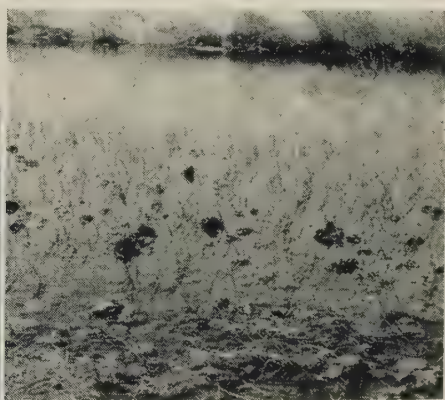


Fig. 39. Close-up of a section of figure 38 at the lowest part of the check. Note beginning of upright rice growth.

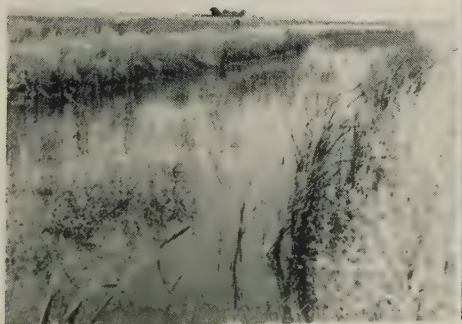


Fig. 40. Rice check on June 14, 1955. Note blank areas without rice.

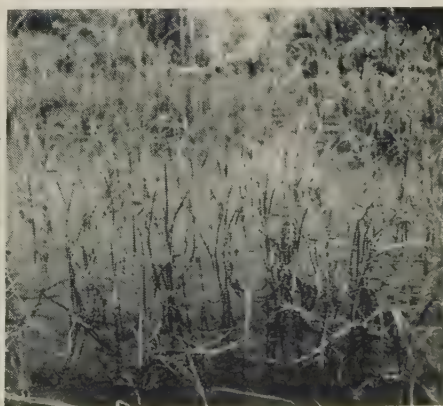


Fig. 41. Close-up of a section of figure 40, showing upright rice growth.

in 1955 because of the occurrence of several of the adverse conditions which affect upright growth. Probably the main factor was the sudden increase in water depth prior to the second sample on May 24. By June 14, 1955, over 90 per cent of the surviving rice plants had at least one upright blade and the majority had three to five (fig. 41). Figure 40 shows the appearance of the study check on June 14. The large blank areas where rice plants failed to survive are clearly visible. The lower water level after this date was due to irrigation failure, but by May 26 the water was back to its earlier height.

It should be pointed out that population counts, temperature recordings, and other observations taken in the check under study do not necessarily apply to all checks in the rice field. The specific site of study was selected as an area which would probably provide suitable situations for leaf miner activity. Similar situations also occurred in many other parts of the field. The rice check studied in 1956 was subject to more favorable conditions than in 1955; in fact, the entire field appeared to have a higher yield potential than the 1955 field.

Trapping records of 1954, 1955, and 1956 (figs. 23 and 24) show a rather sharp decrease in number of adults collected from mid-May to mid-June during the period of early emergent rice growth and extensive leaf-mining activity. Oviposition also follows this same general trend (fig. 24). Since host material was plentiful, it is evident that some other factor or group of factors either prevented a continued buildup or made the habitat unfavorable.

An increase in predators and parasites at this time may have been partly responsible for decreasing adult population, but the extreme maximum temperatures of this period also may contribute to this decrease. The water receives very little shade from vegetation during May and June and consequently its daytime maximum temperature may be quite high. On June 3, 1954, and May 19 of 1955 and 1956, the rise in water temperature coincided with the initial drop in water level. At this time, water temperatures within a single rice check varied considerably, depending on depth, circulation, and air temperatures. An example of this variation was shown when the unshaded temperature of the water (3 to 4 inches deep) in a "barrow pit" was 88° F, but the temperature of the uncirculating water (1 to 2 inches deep) 20 feet across the check was 104° F.

The seasonal maximums of air, water, and radiation temperatures did not always fall on the same date due to water depth, plant growth, and other variables that occur in a rice field. The incidence of three consecutive days in which the air, radiation, and water temperatures were jointly highest occurred from June 21 to 23, 1954; from June 6 to 8, 1955; and, from June 21 to 23, 1956. On June 6, 1955 (air temperature 102° F, water 97° F, and radiation 117° F), several dead flies were observed on the water surface and others exhibited erratic actions similar to those observed under high temperature conditions in the laboratory. The adult trapping records (figs. 23 and 24) were already decreasing or were at a low level at the time of these high temperature periods. If the decrease in population was due mainly

to temperature, then it appears to exert a cumulative rather than a sharply delimiting effect.

High temperatures are undoubtedly a limiting factor in the completion of development of immature forms of the rice leaf miner. The eggs, larvae, and puparia are associated with the leaves and thus are subject to temperature fluctuations of the plant. The temperature of a leaf lying on the water surface will be near the temperature of the upper water layer, but the temperatures of leaves above water, and in the sun, may be much higher than the shaded air temperature. It would be necessary to employ special thermocouple or resistance thermometers to obtain accurate data on leaf temperatures. Because such equipment was not available, the radiation black bulb was substituted to show the same "kind" of temperatures that affect the immature forms. The extent of wind motion over the water surface was also important because of its forced evaporative and cooling effect. The maximum radiation temperatures in the rice field always occurred during very calm or low wind velocity days. Dead and dried larvae and puparia were frequently observed in upright rice blades during the latter part of May and June. Such mortality appeared to be the result of lethal temperatures.

Adults oviposit on rice (at a decreasing rate) from the time of its emergence from the water until the latter part of June and early July. Consequently, all stages of the life cycle of the fly can be found in varying numbers after the completion of the first generation on rice. A review of field observations taken from 1954 through 1956 indicated the possibility of three complete generations on rice, depending on the time of planting and existing temperatures. The first generation of flies usually emerged between the last of May and the first part of June. A second generation, starting the first part of June, completed its development during the latter half of June. The number of second generation flies emerging from rice was always much smaller than that of the first generation. Only a restricted third generation was completed on rice. If some of the immature stages of the third generation were able to survive in the warmer areas of the rice field, then their development was usually completed by the first part of July. Very little mining activity was observed on rice toward the end of June, except in the first or second rice checks from the field water inlet. The water in these checks was usually cooler than the remainder of the field and emergence of the third generation was often extended into mid-July.

A limited amount of development also takes place on certain weeds which emerge with the rice. All immature stages were occasionally found on *Echinochloa crusgalli* (watergrass) and larvae and puparia were found on *Typha latifolia* (cat-tail). It was not unusual to find larvae and puparia in many of the common rice field weeds (the weed species varied somewhat with locality and number of years the field was in rice) because of the larval habits previously mentioned, but the host preference was predominantly rice.

Survival in Limited Areas, July to October

Survival Areas. The prevailing climate of this period is characterized by high daytime maximum temperatures and little or no rainfall (table 12). In the selected rice check of 1955, the radiation and water temperatures (figs. 25 and 26) showed a general decrease from July to October. Air temperatures (fig. 25) were higher than water temperatures because the water was continually receiving shade as the rice plants increased in size.

TABLE 12

DEVIATIONS FROM CLIMATOLOGICAL DATA AT DAVIS, 1953 THROUGH 1956

Period	Mean temperature	Days maximum temperature 100° F or above	Rainfall	Evaporation
	° F		in	in
July				
Average.....	75.0	9 0	0.02	11.01
1953.....	+1.6	+4.0	-0.02	+0.20
1954.....	+2.1	0.0	-0.02	-0.23
1955.....	-1.4	-5.0	-0.02	+0.39
1956.....	-0.5	-2.0	-0.02	-0.06
August				
Average.....	73.5	6.5	0.04	9.82
1953.....	-1.4	-3.5	+0.04	-0.59
1954.....	-3.0	-5.5	+0.04	-0.13
1955.....	+0.8	+0.5	-0.04	+0.83
1956.....	-1.0	-5.5	-0.04	+0.09
September				
Average.....	70.0	5.5	0.25	7.81
1953.....	+3.5	-0.5	-0.25	-0.26
1954.....	-0.4	-5.5	-0.25	+0.33
1955.....	+2.2	+2.5	+0.67	+0.52
1956.....	+1.2	-5.5	-0.25	+0.02

The immature stages of *H. griseola* were rarely found on rice plants by the latter half of July. Most rice plants were 20 to 30 inches in length by that time with their blades well above the water surface. Adults were occasionally observed throughout the rice field from July to October, but were consistently found only in restricted areas of the field.

These restricted localities were limited to the areas which carried well water into the rice field. The pumps continually operated and the water temperature remained nearly constant at 67° F. The water temperature increased as the water drained into the rice field depending on the distance it moved, depth, amount of circulation, et cetera. The ditches leading from the pump (figs. 42 and 44) and areas adjacent to the first rice check into which they drained, remained quite cool. The sharp contrast of temperatures between most of the rice field and the restricted cool areas can be demonstrated by readings taken on August 7, 1955, as follows: permanent rice study check, water temperature 87° F; shaded air temperature 2 inches above water, 91° F; shaded air temperature 5 inches above adjacent levee, 103° F; irrigation ditch carrying well water to the first rice check, water temperature 67° F; shaded air temperature 2 inches above water, 74° F; and shaded air temperature 5 inches above adjacent bank, 90° F.

The low water temperature of the areas was not favorable for rice growth, but several grasses were common and served as host plants for *H. griseola*. *Echinochloa crusgalli* (watergrass) was abundant on the banks and their blades which were touching the water were occasionally mined, but the most important host plant was *Polypogon monspeliensis* (beardgrass). Beardgrass was common on the banks and was well adapted to growing in standing water (figs. 44 and 45). New growth of beardgrass was continually available and found in close association with the water. Its seeds, which fell on floating algae (fig. 45) or floating horned pondweed (fig. 43), would germinate on the water surface and extend their roots to the bottom for permanent anchorage.



Fig. 42. Head of irrigation ditch that received well water (August, 1955).



Fig. 43. Part of a rice check at end of irrigation ditch. Note absence of rice and dominance of horned pondweed in water (August, 1955).



Fig. 44. Exit from an irrigation ditch to the first check of a rice field (August, 1955). Note flowering heads of beardgrass.



Fig. 45. Entrance to irrigation ditch of figure 44. Note floating algal growth and beardgrass.

From June 27 to September 22, 1955, the adult traps and oviposition plants were located in several rice checks and also in the cooler inlet areas. The recordings of figure 24 for this period would be somewhat higher if all the traps and oviposition plants had been located in the cooler areas. A general field distribution was maintained, however, to determine if activity continued in the rice checks following the initial population decrease.

Watergrass and beardgrass were present throughout the rice field from July to October in situations suitable for oviposition and mining, but after the latter part of July, immature stages were found only in cooler areas and were primarily associated with beardgrass. All stages of the life cycle were found during these months, and for this reason no clear-cut generations could be followed. It was estimated, however, that based on growth curves obtained in the laboratory and a knowledge of the temperatures present at these inlet areas, four generations could be completed from the first half of July to the end of September.

Adult trapping records of 1954 (fig. 23) do not show the extent of activity that was recorded from July to September, 1955, because no limited survival areas were found.

Rice fields in several counties of the Sacramento Valley were surveyed for *H. griseola* in August of 1955, to determine if the cool survival areas of the Davis study field were unique or whether they existed in other parts of the valley. All immature stages and adults were found in similar situations in Colusa, Sacramento, Placer, and Yolo counties. The water source of these surveyed areas was from wells or occasionally canals, and water temperature ranged from 60° to 72° F. Beardgrass was found at all of these localities and was the predominant host plant. Areas of no activity were usually associated with high-water temperatures or unfavorable host-plant relationships. Adults were also found in August, on the edges of the American River, Sacramento County; Sacramento River, Yolo County; and the Auburn Ravine Creek, Placer County.

The time of rice harvest varies somewhat throughout California, but in the Sacramento Valley the fields are usually drained in the latter half of September and the rice harvested as soon as possible in October. The fields studied in 1955 and 1956 were drained approximately September 20.

Fall Dispersal and Overwintering, October to January

Habitat Changes and Dispersal. The cessation of rice-field irrigation by the end of September, eliminated many areas where *H. griseola* had been continually active since July.

Air, radiation, and water temperatures were steadily decreasing during the fall months and maximum temperatures were no longer an important factor in restricting adults to specific areas. Fall rains (table 13) in September, October, and November, of the years under study, were usually not heavy enough to form standing pools, but they caused germination of grasses which by mid-December attained a height of 3 to 6 inches. Grasses were mature and fairly abundant in certain situations, such as permanent streams, ponds, sewage ditches, and temporary irrigation drainage ditches.

TABLE 13

DEVIATIONS FROM CLIMATOLOGICAL DATA AT DAVIS, 1953 THROUGH 1956

Period	Mean temperature	Days maximum temperature 70° F or above	Days minimum temperature below 30° F	Rainfall	Evaporation
	° F			in	in
October					
Average.....	62.5	27.0	0.5	0.78	5.05
1953.....	+0.6	+3.0	-0.5	-0.62	+0.73
1954.....	+0.5	+3.0	-0.5	-0.78	+0.90
1955.....	+1.8	+4.0	-0.5	-0.34	+0.30
1956.....	-0.2	-3.0	-0.5	-0.24	-0.30
November					
Average.....	52.5	10.5	1.5	1.62	2.40
1953.....	+1.8	-5.5	-1.5	+0.15	-0.83
1954.....	-0.8	-4.5	-0.5	+1.36	-0.75
1955.....	+0.2	-1.5	-1.5	-0.46	+0.33
1956.....	+1.4	+2.5	-1.5	-1.55	+0.73
December					
Average.....	46.0	1.5	5.0	3.25	1.15
1953.....	+3.1	-1.5	-1.0	-3.04	+0.85
1954.....	-2.3	-1.5	-5.0	+0.66	-0.22
1955.....	+3.8	-1.5	-5.0	+8.62	-0.22
1956.....	-1.3	-0.5	+6.0	-3.08	+0.31

An occasional adult was observed at many of the above-mentioned aquatic areas during October and November of 1954, 1955, and 1956. No flies were found in most of these situations during the summer because of high maximum temperatures. Their presence in the fall, therefore, indicates a dispersal from the restricted summer breeding areas. In places where water was permanent and host plants were available, eggs were usually laid to initiate a fall generation.

Two areas were studied by means of adult traps in the fall of 1955. A permanent pond was created on the Davis campus on September 1, and it was abundantly supplied with transplanted beardgrass. Adults were first caught on October 25, and eggs and first instar larvae were also observed on this date. Mining became more extensive and puparia were observed by November 21. All stages of the life cycle were continually observed following this date and the increase in population is shown in the single trap record given in figure 27. It was necessary to supply a continuous water flow to maintain the water level of the pond, which was located on rather light, porous soil. The water source remained fairly close to 70° F (fig. 27) and, consequently, development of the immature stages occurred at a faster rate than under normal field conditions for this time of year.

The second study area was located at one of the well-water pumps of the same rice field that was observed during 1955. A permanent pond was created by blocking one end of the ditch leading from the pump, and water was added periodically to maintain the water level. The grasses at this pond (predominantly beardgrass) were being mined at the time the rice field was drained, so activity was uninterrupted because the pond was created immediately following drainage. Adults were collected in traps at this pond

until November 27 (fig. 24), but the latest egg deposition was recorded on October 28. Puparia were periodically collected from beardgrass in the pond and retained in floating wire-screen cages. Emergence in these cages was observed through October and November, the last occurring November 25.

Overwintering. Mean maximum water and air temperatures at the rice-field pond varied between 50° and 55° F during the latter half of November and the entire month of December, 1955. No adults were caught at the pond and no immature stages were found on the remaining pond grasses. Unfortunately, most of the grasses closely associated with the water surface were destroyed by muskrats. Mining activity probably would have continued, at least at a very slow rate, if grasses had been abundant during the rest of the year. To determine if pupal development would be continuous under the field temperatures of this period, newly formed puparia (from the pond on the Davis campus) were transferred to screen cages on the rice-field pond November 30. Flies emerged from these puparia on December 28, 29, and 30, which shows that there was no cessation of development. Mean water temperature for this period was approximately 50° F, and the development time for these field-located puparia approximated that of laboratory-reared puparia held at a constant temperature of 50° F.

Late November and December rains are often sufficient to create shallow, standing pools and a few adults were observed on some of these pools near Davis, on December 7, 1954, and December 11, 1955. New grass growth was usually associated with them and newly laid eggs were found on the grass both years. Shaded air temperatures at the time of these observations were 58° and 60° F. These areas were later flooded by heavy rains, so further observations were impossible.

Limited observations were also made at Putah Creek in the lower Coast Range foothills (altitude approximately 250 feet), 16 miles east of Davis. Numerous adults were found in October and November of 1954 through 1956. In 1956 a section of the creek that contained an abundant growth of beardgrass was located, and the first fall generation began emerging from this grass on approximately November 28. All stages of the life cycle were observed from this date until January 7, 1957, at which time a final observation was made in the area. Water temperatures, at the time of these observations, ranged from 43° to 49° F, and shaded air temperatures ranged from 52° to 65° F.

Collections and observations from October to January showed that when a suitable habitat was available a fall generation was completed by the end of November. A limited amount of oviposition indicated the start of a second generation the last part of November and early December. It is not known if this second generation was completed except under the favorable conditions previously mentioned, and because of low temperatures, it is doubtful if emergence could occur before the last of February or early March.

During the period extending from September to February, adults were found more frequently than any other stage of the life cycle. It is the author's opinion that the start of the first year's generation during the last half of January and February begins with adults that previously emerged from September to the last half of November. This opinion is based

on the field observations previously mentioned and data obtained from laboratory experiments concerning adult longevity and adult resistance to low temperatures. All immature stages observed during this time showed continuous development at a rate normal for the temperatures present.

Review of Seasonal Generations

H. griseola is a multivoltine species in which the number of generations occurring in a given area are dependent primarily upon the temperatures of that area, host plant availability, and suitable high moisture conditions.

All stages of the life cycle could generally be found after the completion of the first generation of the year. The changes in habitat and host plants

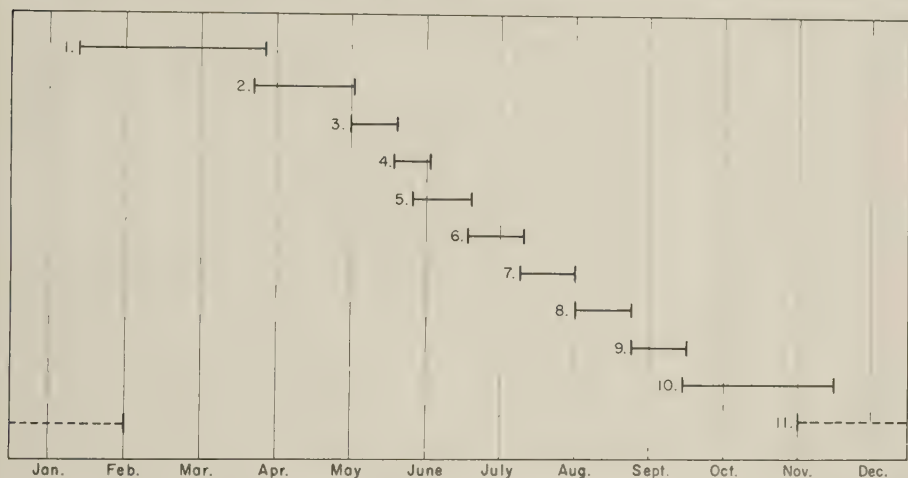


Fig. 46. Theoretical maximum number of annual generations and approximate duration of these developmental periods of *Hydrellia griseola* at Davis.

throughout the year served as reference points for the beginning of new generations, and periodic examination for emerged puparia indicated completion of generations. When species activity was concentrated in one area for several months, and on one type of host plant, the estimation of completed generations was made by reference to the temperatures of that area, and the rate of development as determined in the laboratory.

Figure 46 presents a graphic display of the theoretical maximum number of generations and their approximate development periods. They can be grouped by habitat and host as follows: (1) field grasses associated with rainfall; (2) field grasses mainly associated with rice-field irrigation; (3) to (5) rice plants and rice-field weeds; (6) to (9) mainly beardgrass and watergrass associated with rice-field cool water inlets; (10) late summer field grasses associated with permanent streams, ponds, and drainage areas; and (11) possible carry-over on early fall field grasses associated with late fall rains.

Monthly totals of adult trap catches and records of pupal emergence occasionally showed one sex to be slightly more abundant than the other, but

the sex ratio was sometimes reversed during the same month of the following year. A sex ratio based on the total trap catches for three years (more than 5,000 flies) was 1.3 males to 1.0 females.

NATURAL ENEMIES

Hymenopterous Parasites

It is quite common for leaf mining insects to have numerous parasites, and *Hydrellia griseola* is certainly no exception. A review of literature and the present investigations have shown the rice leaf miner to be parasitized by a possible 34 species included in six families. The majority of these species fall within the families Braconidae and Eulophidae, but the braconid species are usually found in greater abundance and appear to be the most important natural enemies.

Kuwayama *et al.* (1955) reported the following parasites of *H. griseola* from Japan. Of the total, they considered the genera *Opius* and *Chorebus* to be the most effective.

Family Braconidae

Chorebus sp.

Merites ? sp.

Opius sp.

Family Ichneumonidae

Hemiteles sp. (considered a secondary parasite)

Family Eulophidae

Asecodes sp.

Elachertus ? sp.

Mestocharis ? sp.

Neochrysocharis sp.

Paracrias sp.

Rhopalotus sp.

Solenotus sp.

Family Proctotrupidae

Ismarus sp.

Family Pteromalidae

Merismus sp.

Trichomalus sp.

Parasites reported from Europe are limited to the two families listed below.

Family Braconidae

Ademon decrescens Nees. (Séguy, 1934).

Ademon sp. France. (Nepveu and J. D'Aguilar, 1951).

Coelinus hydrellia Kawall, 1867. Latvian S.S.R.

Chorebus uliginosa Nees. Germany. (Described as *Gyrocampa thienemanni* Ruschka, 1913, but host determination has been questioned.)

Chaenusa conjugens (Nees.) France. (Risbec, 1952, reported on the synonym *Hydrellia incana*.)

Opius punctiventris Thomson. (*Supra cit.*)

Family Eulophidae

Chrysocharis sp. France. (Risbec, 1952, hyperparasites of the synonym *Hydrellia incana*.)

In South America, Parker *et al.* (1951-52) listed three species of parasites of *H. griseola* (Ex. rice leaves) from Uruguay.

Family Braconidae

Opius sp.

Family Eulophidae

Achrysocharis sp.

Family Pteromalidae

Pteromalus sp.

Parasitic species in four families are represented in North America. These species are listed below with comments on their known distribution as parasites of *H. griseola*, and relative abundance as determined by collections during these investigations or those of Lange in 1953. All specimens were determined by B. D. Burks or C. F. W. Muesebeck of the United States National Museum, unless otherwise indicated.

Family Braconidae

Chaenusa sp. (probably *C. conjugens* Nees.) Madison, California. July, 1953. One specimen.

Chorebus aquaticus Muesebeck, 1950. California. Common.

Chorebus sp. (Malloch, 1915, as *Gyrocampa* sp.) Illinois.

Opius hydrelliae Muesebeck, 1933. California, Oregon. Common.

Family Diapriidae

Trichopria columbiana (Ashmead), 1893. Gridley, California. July, 1953. One specimen.

Trichopria sp. Davis, California. May, 1955. Two specimens.

Family Eulophidae

Derostenus sp. Davis, California. April, 1955. Two specimens.

Pnigalio sp. Davis, California. April, 1956. One specimen.

Solenotus intermedius (Girault), 1916. Davis, California. April, 1956. Eleven specimens.

Sympiesis sp. Davis, California. April, 1956. One specimen.

Family Pteromalidae

Eupteromalus americanus Gahan, 1933. Davis, California. June, 1955. Four specimens.

Eupteromalus sp. Colusa and Sacramento, California. July, 1953. Five specimens.

Halticoptera sp. Davis, California. April, May, June, 1954-1956. 63 specimens.

Seasonal Abundance, Known Biology, and Extent of Parasitism. Members of family Eulophidae were found only during the spring months. *Derostenus* sp. is believed to be a continuous, solitary, internal feeder on the host-larvae because of the wasp's emergence from dead third instar larvae of *H. griseola*. *Pnigalio* sp., *Sympiesis* sp., and *Solenotus intermedius* are believed to be external larval feeders as they pupated free of their host.

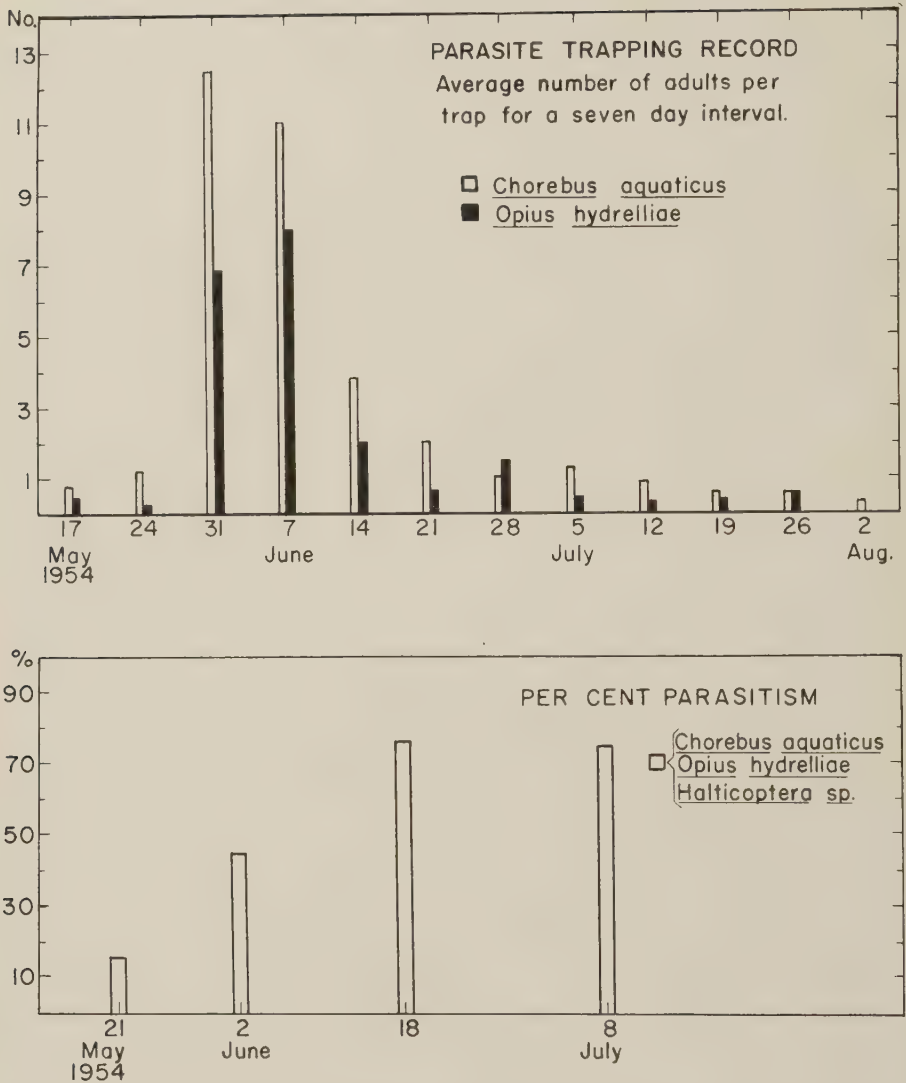


Fig. 47. Adult parasite trapping record (based on four traps) and per cent parasitism as determined by emergence of the parasite and examination of *Hydrellia griseola* puparia, collected near Davis. The number of leaf miner pupae collected at the sampling dates was as follows: (chronological order) 94, 11, 25, and 8.

S. intermedius was first reported as a parasite of the agromyzid fly *Phytomyza chrysanthemi* (Girault, 1916). Parasitic activity of species of these last three genera was observed quite extensively in the last half of March and first part of April in 1956. Microscopic examination of mined grasses showed parasite eggs in abundance and from one to four parasitic larvae feeding externally on a single *H. griseola* larvae. The samples were taken from grasses associated with rain pools, and there appeared to be a relationship between

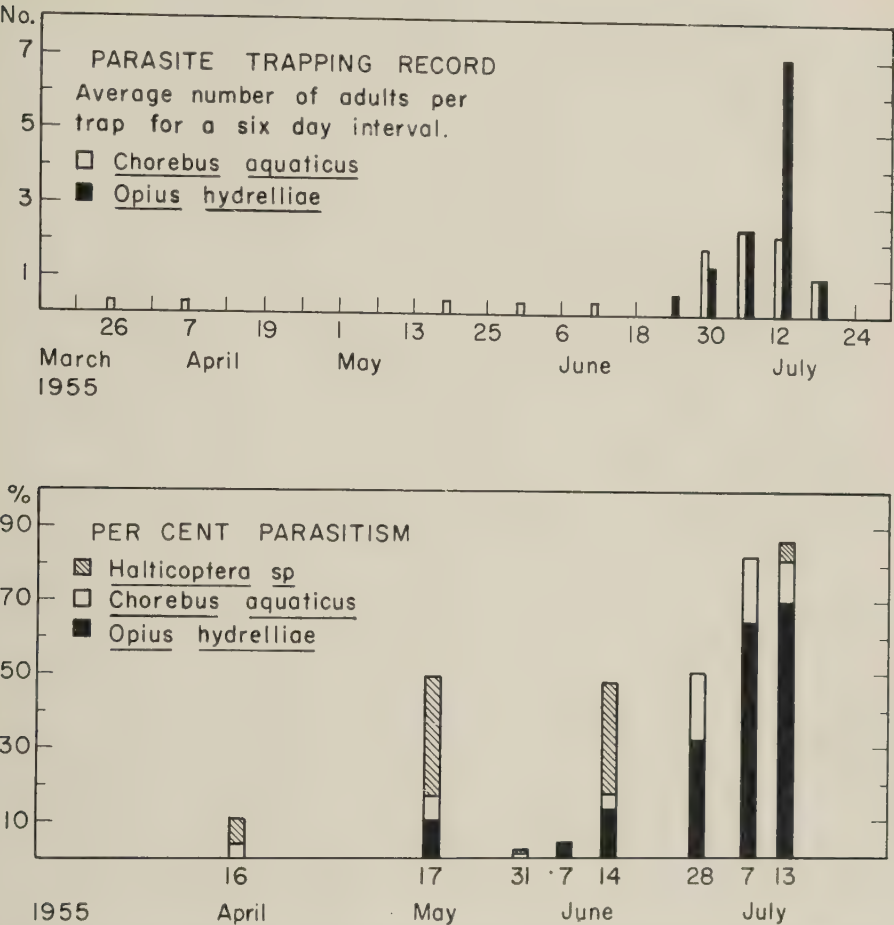


Fig. 48. Adult parasite trapping record (based on the four highest of six traps), and per cent parasitism as determined by emergence of the parasite and examination of *Hydrellia griseola* puparia, collected near Davis. The number of leaf miner pupae collected at the sampling dates were as follows: (chronological order) 71, 193, 439, 82, 27, 171, 58, and 23.

the abundance of external-feeding, larval parasites and the amount of water remaining in the drying pools. Parasitism was repeatedly higher in those areas that were nearly dry than at pools having several inches of water. One sample revealed at least one external-feeding parasite larva on 60 per cent of the *H. griseola* larvae. This percentage was based on counts of 30 host larvae in 10 leaves.

Collections of parasites of the family Diapriidae were rare and limited to the genus *Trichopria*. Lange reared a single specimen of *T. columbiana* from Gridley, California, in 1953. Berg (1950) reported this species parasitizes *Hydrellia ascita*, *H. bergi*, *H. luctuosa*, *H. pulla*, and *H. curalis* in Michigan. Two specimens of a probable second species, determined as *Tri-*

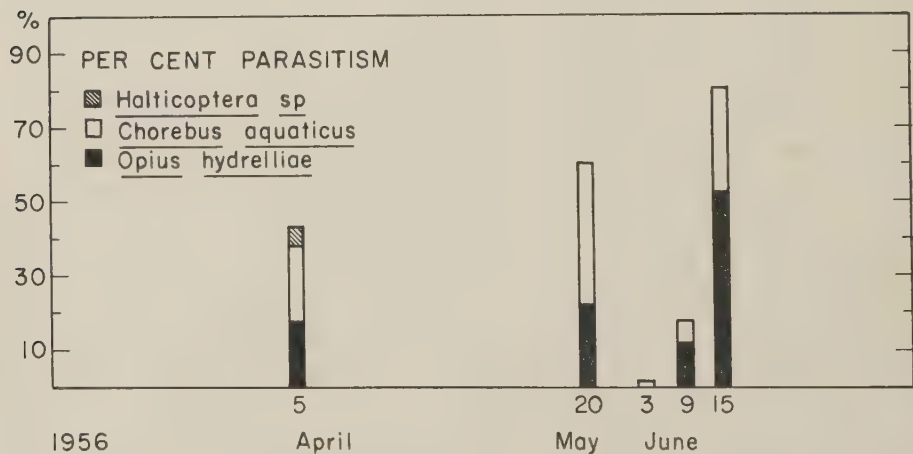
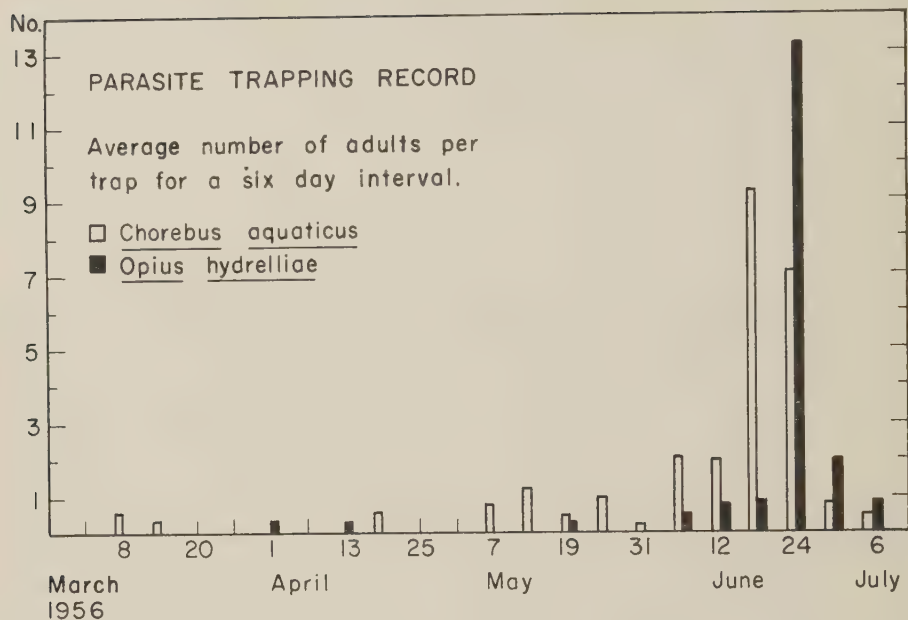


Fig. 49. Adult parasite trapping record (based on the four highest of six traps), and per cent parasitism as determined by emergence of the parasite and examination of *Hydrellia griseola* puparia, collected near Davis. The number of leaf miner pupae collected at the sampling dates was as follows: (chronological order) 28, 43, 105, 17, and 15.

chopris sp., were reared at Davis in May of 1955. All three specimens were reared from the puparia of *H. griseola* and are assumed to be internal larval feeders.

The Pteromalid species *Eupteromalus americanus* was rather scarce and was found only in 1955. It is probably a solitary, internal larval feeder as it emerged singly from the puparium of *H. griseola*. Previously it had been

listed as a parasite of *Phytophaga destructor* (Gahan, 1933). Lange reared five specimens of this genus, determined as *Enteromalus* sp., from *H. griseola* puparia that were collected at Colusa and Sacramento, California, in 1953. *Halticoptera* sp. was the third most abundantly collected parasite of *H. griseola*. It is an internal parasite of the larva of the rice leaf miner and emerges through the puparia. Figures 48 and 49 show its abundance relative to the braconid species, as determined by pupal collections in 1955 and 1956.

The family Braconidae contains three species from California which are parasitic on *H. griseola*, and probably is the most important family in exerting varying degrees of natural control of the rice leaf miner. All three species are internal parasites of the host larvae and emerge through the puparia.

Chaenusa sp. is quite rare and known only from a single specimen reared by Lange from Madison, California, in July of 1953.

Chorebus aquaticus was originally described from Sacramento, California, in 1941, but was collected as early as 1923. It is recorded in Butte, Colusa, Sacramento, San Joaquin, and Yolo counties, but it probably extends throughout the rice-growing areas of California. *C. aquaticus* was also reared from the puparia of an undetermined *Hydrellia* species, mining horned pondweed, at Davis in October, 1955.

Figures 47 to 49 show collections of *C. aquaticus* in 1954, 1955, and 1956 taken with the same traps used to collect *H. griseola* adults. These figures also show the per cent parasitism by *C. aquaticus* as determined by periodic host-pupal collections in 1955 and 1956. In addition to the periods covered by the charts, *C. aquaticus* was reared from *H. griseola* puparia from August through October of 1955 (complete range, April to October), and also collected in traps from August through November (complete trapping range, March to November). The per cent of parasitism was not given for these late summer and fall months because of the small sample of puparia available for collection. The *C. aquaticus* collected in the traps never averaged more than one per trap during this time. A specimen of *C. aquaticus* also emerged from a *H. griseola* puparium in the laboratory on January 7, 1957.

Opius hydrelliae was originally described from Sacramento, California, in 1933. It has been collected in Butte, Colusa, Sacramento, San Joaquin, Tulare, and Yolo counties of California. *H. griseola* is the only recorded host of *Opius hydrelliae*. Trapping records and per cent parasitism by this species are also presented in figures 47 to 49 for various periods of the years 1954 through 1956. In addition to the recordings of the above figures, *O. hydrelliae* was reared from puparia in August, and one specimen emerged on January 3 in the laboratory. The fly puparium which produced this wasp in January was placed in the field on November 30, 1955, and removed to the laboratory three days prior to emergence. *O. hydrelliae* was collected in traps during the months of March through August and also the latter part of November.

Figures 47 to 49 show that interspecific competition of the parasites for the host *H. griseola* varied from year to year. Detailed information is lacking on the full effect exerted by the species belonging to the family Eulophidae, but known information indicates that their greatest influence was

upon the first and second generations of *H. griseola*, which were mining the wild grasses. Trapping records of *Halticoptera* sp. were not kept, but rearings from host pupae show its greatest influence on the first and second host generations. It was most abundant in 1955 when its parasitism extended into the third host generation, which was mining rice. It was also active during the rice season of 1954, but unfortunately the records of the proportion of individual species parasitism were lost, and only total parasitism is presented (fig. 47).

The braconids, *Chorebus aquaticus* and *Opius hydrelliae*, were ultimately the most abundant parasitic species during the years 1954 through 1956. Trapping records indicated the presence of larger numbers of *C. aquaticus* in 1954, but *O. hydrelliae* was more frequent in the traps and rearing of 1955 and 1956. The general trend indicates that *C. aquaticus* is more active in the early part of the year and eventually is surpassed by *O. hydrelliae*. The trapping records (1954–1956) consistently show the maximum peak of activity of *O. hydrelliae* to be approximately one week following that of *C. aquaticus*.

The combined parasitism data show the typical host-parasite (or predator) curve in which the maximum density of parasites follows that of the host. The rearing records of 1955 and 1956 show a double oscillation. The first peak or subpeak was the result of parasitism upon the first and second host generations (on wild grasses), and rose to 50 and 60 per cent parasitism. Parasitism of the beginning of the third host generation (first generation on rice) dropped to 2.5 and 1.0 per cent (figs. 48 and 49), but increased on the following host generations to 87 per cent in 1955 and 80 per cent at the termination of investigations in 1956. Studies in 1954 showed a similar rise in parasitism to 76 per cent, but parasitic activity was not determined on the host generations mining wild grasses prior to rice. Rate of parasitism dropped sharply after mid-July because of the previous decrease in host density.

The reasons for the drop in parasitism when the flies change their main host plant to rice are not fully known. Distance alone is not a reason because the parasites are active previous to this in the grasses of ditches and drainage areas closely associated with the rice fields, as well as the grasses on the levees within the rice fields. A possible explanation may be that the parasites are not as well adapted as the host to activity on the vast open water areas of a rice field of young emerging plants.

The low rate of parasitism on the host's initial infestation of rice may appear to minimize its economic importance. It must not be overlooked, however, that the extent of parasitism on the two generations previous to those which attack rice usually eliminates over half of the potential host population.

Miscellaneous Enemies

A rice field abounds with numerous invertebrate and vertebrate species which may directly or indirectly be concerned with the ecology of the rice leaf miner. A detailed study was not made of all possible interactions, but some of the more obvious or potentially detrimental relationships that may affect the abundance of *H. griseola* are mentioned below.

Small, brightly colored red mites belonging to the family Hydryphantidae were often observed attached to *H. griseola* adults in rice fields near Davis. These mites were viewed in June and July of 1955 and 1956, and adult flies were collected with from one to six mites attached to various parts of the body. Specimens of these mites were sent to R. W. Mitchell of the University of Vermont and tentatively determined as mite larvae of the genus "*Hydryphantes?*" If their life history is similar to that of other water mites (Pennak, 1953), then the adult is free-living in the water. Its eggs hatch and the active larvae seek a host at the substrata or surface film and assume an ectoparasitic existence. After a variable feeding period, the larva begins to metamorphose to a quiescent nymphophan and then leaves the host as an active nymph to pass through the stage of quiescent teleiophan to adult. The number of mites necessary to produce mortality of their host or their host specificity is not known, but similar mites were observed on several dipterous species associated with the water.

Numerous spiders belonging to the family Lycosidae were commonly observed throughout most of the year in the same habitat as adults of *H. griseola*. They are known as wolf spiders, as they do not spin a food-catching web, but actively chase down their prey. They easily move across the water surface and bordering grasses, and quite often have been observed stalking *H. griseola* adults. Several captures were witnessed and even though a detailed study was not made, the abundance and aggressive behavior of the spiders lead the author to consider them an important predator. Periods when the flies would be particularly vulnerable, would be just after pupal emergence until flight is possible, during copulation, and when the female is ovipositing. Spiders increased in abundance as the rice fields matured and by the last part of June and July, more spiders were caught in the floating traps than *H. griseola* adults. The dominant lycosid species at this time was *Pardosa ramulosa* McCook (determined by W. J. Gertsch), which is one of the most common members of its group in California.

Muskrats are quite common in California, and during certain times of the year, when aquatic habitats are rather limited, they may indirectly be considered an enemy of *H. griseola*. The muskrats live and multiply in the rice fields during the summer, and they move to permanent aquatic areas such as ponds and drainage areas after the rice fields are drained. They feed on grasses associated with the borders of their aquatic environment. When abundant, they may nearly eliminate those grasses that are being mined, as well as the potential host plants of *H. griseola*. Such a situation occurred at the small pond created in a drained rice field near Davis, in the fall of 1955. A trapping effort to eliminate them yielded 16 muskrats in the course of two and one-half months at the small pond.

YEARLY INTERACTION OF ECOLOGICAL FACTORS

Climatic conditions during the first three months of the year are nearly all favorable for a buildup of the rice leaf miner. Occasional below-freezing temperatures occur, but generally they are of short duration and do not appear to be detrimental. Increasing maximum temperatures lengthen adult activity periods and shorten developmental time. Monthly rainfall is decreas-

ing, but the seasonal maximum occurs during this period, and the area has numerous standing rain pools. Wild grasses have been increasing in abundance and growth since fall and are generally found in close association with the rain pools.

The habitat from March to May begins to decrease in suitability. The rising temperatures and increased evaporation rate, coupled with decreasing rainfall, greatly reduces the number and size of the standing rain pools. Many of the wild grasses that formerly had their blades lying on the water or in close association with it, are now well above water or lying on the moist soil. Consequently oviposition is greatly reduced and some mining is interrupted. Parasitism gradually increases during this period by nearly all parasitic species. Members of the family Eulophidae appear to exert their greatest effect at this time.

H. griseola activity begins to increase during the latter part of April and the first half of May because of the creation of a favorable habitat by the irrigation practices of rice culture. Oviposition and mining activity are at their maximum by mid-May, as most of the rice plants have emerged through the water. Continued leaf miner development on rice depends mainly on the rate of rice growth. Cool temperatures, deep water, high winds, and abundant algal growth are all factors having a tendency to retain the rice blades on the water surface. The converse of these factors is usually associated with rapid rice growth and decreased miner activity.

The rate of parasitism has been consistently low on the first host generation mining rice, but rapidly rises to between 80 and 90 per cent by July. The most abundant parasitic species at this time are *Opius hydrelliae* and *Chorebus aquaticus*.

Maximum June temperatures exert an adverse effect upon *H. griseola* not only by possible direct lethal action on all stages, but also by indirect effects through an increase in rice growth and associated reduction of preferred oviposition sites. Mining of rice is reduced to a minimum by the first half of July, and activity is usually limited to wild grasses at the cool inlet areas of rice fields which are associated with well or river water.

From July through September, limited generations are continued on wild grasses at these cool inlet areas. Parasitism usually declines, and remains at a low incidence for the rest of the year. The rice fields are commonly drained during the latter part of September, a procedure which eliminates the survival areas used by the species to withstand the maximum summer temperatures.

The decreasing temperatures of fall permit adult dispersal to more permanent aquatic areas and a fall generation is usually completed on the grasses in these areas by December. Fall and early winter rains germinate new grasses and begin forming rain pools. There is an indication that a late-fall generation begins in these new areas, but evidence of its completion is lacking. Adult flies were observed from November through January when temperatures were sufficiently high to permit activity, and presumably this is the principal stage of the insect carrying through the winter.

Figure 50 diagrammatically represents the interaction of some of the main ecological factors discussed in this section. *H. griseola* activity and

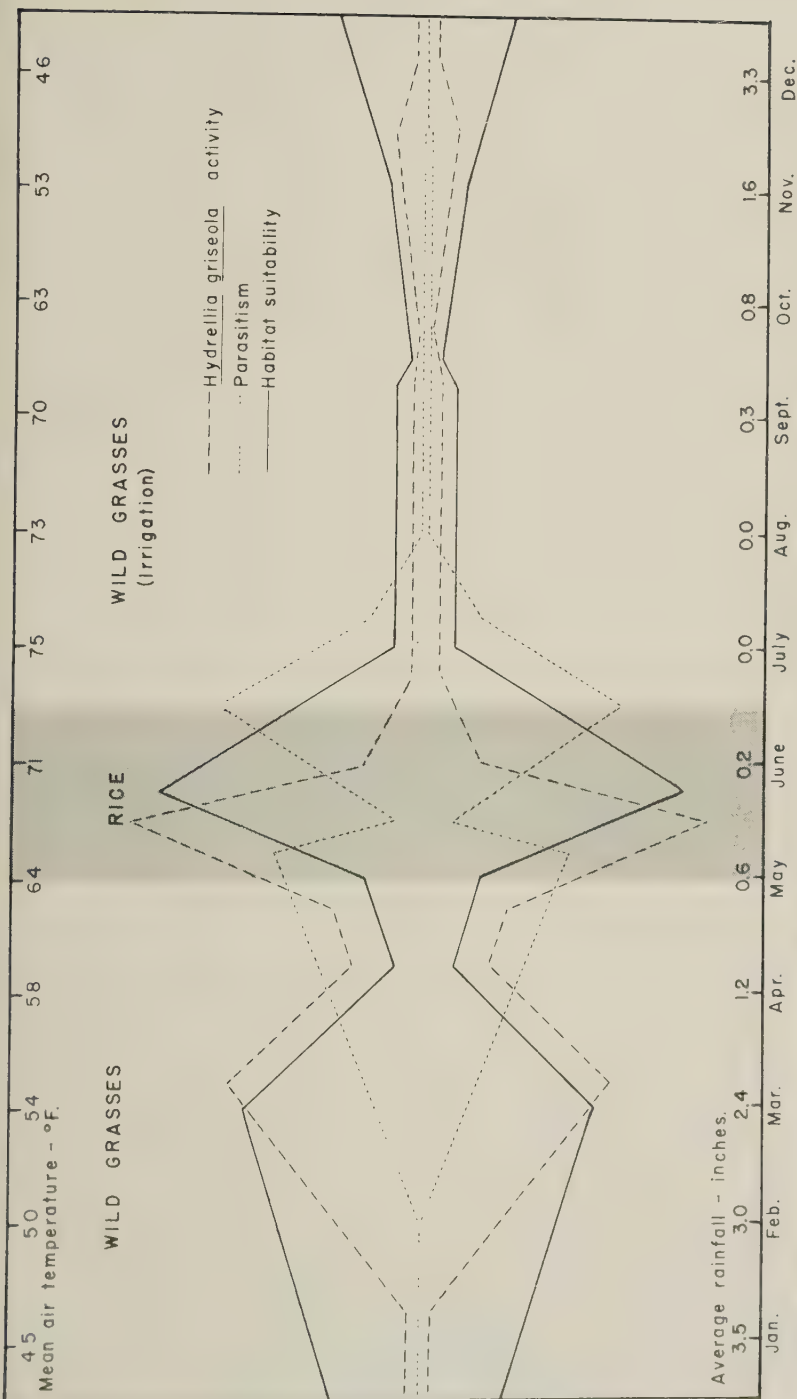


Fig. 50. Diagrammatic representation of the yearly interaction of ecological factors affecting the activity and abundance of *Hydrellia griseola* at Davis.

abundance are based on trapping records, oviposition plants, and general field observations of all the stages of the life cycle, but special emphasis is placed on the adult stage. Parasitism is based on trapping records, host-plant examination, and host-pupal rearings. The expression of habitat suitability is based primarily on host-plant abundance in relation to a suitable water source.

CHEMICAL CONTROL

Successful chemical control procedures for the rice leaf miner were developed by W. H. Lange in 1953. Present control recommendations by the University of California are based on the 1953 work and subsequent field trials.

The most effective time to apply chemicals is during the period just after the rice has emerged from the water. The need for chemical application is governed by severity of attack. *H. griseola* generally does not uniformly infest a rice field because of the many variables previously mentioned. Therefore, a general field survey for damage should be made before chemical control is recommended. Particular attention to field inspection should be made if the weather is cool and the rice growth is slow.

Dieldrin or heptachlor (four ounces of actual chemical per acre) are usually applied by airplane as an emulsible concentrate. **These materials are hazardous to fish and wild life, and chemical drift should be kept to a minimum.** The treated water should be restricted to the rice fields for two weeks following application.

SUMMARY

Larvae of *Hydrellia griseola* were first reported mining rice leaves in California in 1922. Their presence in rice was noted several times hence, but in 1953 their damage was reported throughout most of the rice-growing areas of the state.

The present field study of *H. griseola* was concentrated in the Sacramento Valley and mainly in the vicinity of Davis from 1954 through 1956. Adult traps and oviposition plants were used during the greater part of this study as population indicators. Meteorological information taken in association with the trapping and oviposition records included air, water, and radiation temperatures.

H. griseola adult activity was noted as early as the latter part of January or the first part of February at rain pools bordered with grasses. Oviposition and mining steadily increased in these areas until the latter part of March when the pools began to dry up. The first generation is usually completed during the first half of April.

The second generation usually occurs on grasses in association with rice-field irrigation practices and generally reaches completion in mid-May when the rice is emerging. Adult population and oviposition indices were consistently near their peak at this time. Oviposition starts on rice as soon as it emerges from the water and mining soon follows. A maximum of three generations was found on rice, but each generation was progressively smaller in extent due to adverse maximum temperatures, parasitism, and rapid rice growth.

Adult population and oviposition indices were quite low by the first part of July and leaf-miner activity was almost entirely restricted to the cooler inlet areas associated with wells where water temperatures remained close to 67° F. Observations and existing temperatures indicated the probable completion of four generations, mainly on beardgrass, prior to drainage of the rice fields in September.

Decreasing fall temperatures permit a dispersal to more permanent aquatic areas and a generation is usually completed on grasses in these areas by the latter half of November. Adult flies were observed from November through January and presumably are the main stage of winter carry-over.

Twelve species of parasites were found in California with representatives in four families. The most abundant parasitic species were *Chorebus aquaticus*, *Opius hydrelliae*, and *Halticoptera* sp.

Laboratory studies of the adult showed a decided preference for cool temperatures and high moisture conditions. Adults remained alive as long as 42 days at 28° F, but thermal death began at 108° F at a 4- to 5-minute exposure. Maximum longevity of 146 days occurred at room temperature (49–76° F).

Time-temperature development curves were obtained for the egg, larval, and pupal stages at 5 to 6 constant temperatures. The sum of developmental times of all immature stages ranged from 92.7 days at 50° F to 13.8 days at 90° F.

ACKNOWLEDGMENTS

I am particularly indebted to Dr. W. H. Lange for suggesting the problem in 1954 and for his constructive criticism and active participation throughout the period of research and during the writing of this paper. My sincere gratitude and appreciation are extended to Dr. S. F. Bailey and Dr. Milton A. Miller for their valuable criticism and for the time they devoted to reading this manuscript. I am grateful for the coöperation of Dwight Finfrock of the Rice Experimental Station, and the aid received by the California Coöperative Rice Research Association. Thanks are extended to Dr. H. B. Shultz for the use, advice, and maintenance of meteorological equipment; to Drs. P. W. Oman, W. W. Wirth, B. D. Burks, C. F. W. Muesebeck, W. J. Gertsch, and R. D. Mitchell for the identification of specimens.

LITERATURE CITED

- ASHMEAD, W. H.
1893. Monograph of the North American Proctotrypidae. U. S. Natl. Mus. (45):472 pp.
- BALACHOWSKY, A., and L. MESNIL
1935. Les insectes nuisibles aux plantes cultivées. Tome Premier. Paris, xvi + 1137 pp.
- BECKER, T.
1896. Dipterologische Studien IV, Ephydridae. Berlin. Ent. Ztschr. 4:91-267.
1926. Ephydridae. Die fliegen der Palaeartischen Region. Stuttgart, 6(56a). 115 pp.
- BERG, C. O.
1950. *Hydrellia* (Ephydridae) and some other acalyptrate Diptera reared from *Potamogeton*. Ent. Soc. Amer. Ann. 43:374-398.
- BRIGGS, L. T., and H. L. SHANTZ
1917. Comparison of the hourly evaporation rate of atmometers and free water surfaces with the transpiration rate of *Medicago sativa*. Jour. Agr. Res. 9:277-92.
- BRISCHKE, C. O. A.
1881. Die Blattminirer in Danzig's Umgebung. Schr. der Naturf. Gessell. in Danzig n.s. 5(2):233-90.
- CARTWRIGHT, W. B., R. A. BLANCHARD, and C. C. WILSON
1933. Notes for 1932 on cereal and forage insects in California. California Dept. Agr. Monthly Bul. 22(2-3):156-60.
- CRESSON, JR., E. T.
1932. Studies in the dipterous family Ephydridae. Paper IV. Amer. Ent. Soc. Trans. 58: 1-34.
1944. Synopses of North American Ephydridae (Diptera). Parts IA and II. Amer. Ent. Soc. Trans. 70:163-80.
- DEONG, E. R.
1922. A rice leaf-miner. Jour. Econ. Ent. 15:432.
- ENGELHART, V.
1936. Flies injurious to cereals in the Far East Province. Plant Proc. fasc. 11:154 (Abst. in R. A. E. Ser. A.)
- ESSIG, E. O.
1926. Insects of Western North America. Macmillan Co., New York, ix + 1035 pp.
- FALLEN, C. F.
1813. Beskrifning Öfver några i Sverige funna Vattenflugor (Hydromyzides). Kongl. Svenska Vet. Akad. Handl. 34:240-57.
- FÉRON, M., and H. AUDEMARD
1956. Notes sur *Hydrellia griseola* (Dipt. Ephydridae), mouché mineuse du riz en France. Ann. des Epiphyt. 7(3):421-30.
- GAHAN, A. B.
1933. The Serphoid and Chalcidoid parasites of the Hessian Fly. U. S. Dept. Misc. Publ. (174):148 pp.
- GIRAULT, A. A.
1916. Descriptions and observations on some Chalcidoid Hymenoptera-II. Canad. Ent. 48(8):265-68.
- GRAHAM-SMITH, G. S.
1930. Further observations on the anatomy and function of the proboscis of the blow-fly *Calliphora erythrocephala* L. Parasitology 22(47):115.
- GRUNBERG, K.
1910. Diptera, Zweifluger. Die Süßwasserfauna Deutschlands de A. Brauer. (2a): 273-82.
- HENNIG, W.
1943. Übersicht über die bisher bekannten Metamorphosestadien der Ephydriden, mit Neubeschreibungen nach dem Material of Deutschen Limnologischen Sundaexpedition. (Diptera: Ephydridae). Arb. über Morph. u. Taxonom. Ent. 10(2/3):105-38.
1952. Die Larvenformen der Dipteren, 3 Teil. Akademie-Verlage, Berlin, vii + 628 pp.
- HERING, E. M.
1951. Biology of the leaf miners. Uitgeverij Dr. W. Junk, 's Gravenhage, iv + 420 pp.

HERING, M.

- 1935-37. Die Blattminen Mittel—und Nordeuropas—einschliesslich Englands. Neubrandenburg, iii + 631 pp.

ISAEV, S. I.

1931. Insects injurious to onions in the Rostov District. Bul. Inst. Control. Pests and Diseases (1):25-53. (Abst. in R. A. E. Ser. A.)

JOHANNSEN, O. A.

1935. Aquatic Diptera. Part II Orthorrhapha-Brachycera and Cyclorhapha. Mem. Cornell Univ. Agr. Exp. Sta. 177:62 pp.

JONES, B. J.

1906. Catalogue of Ephyrididae, with bibliography and descriptions of new species. Univ. Calif. Pubs. Tech. Bul. 1(2):153-98.

KAWALL, J. H.

1867. Miscellanea Entomologica. Stettin. Ent. Ztg. 28:120-21.

KIRCHNER, O.

- 1906-07. Die Krankheiten und Beschädigungen unserer landwirtschaftlichen Kulturpflanzen. Stuttgart, 2 ed., x + 625 pp.

KÖRTING, A.

1931. Ueber die Entwicklung der grauen Gerstenminierfliege (*Hydrellia griseola* Fall.) bei verschiedener Ernährung. Zeitschr. Pfl. Krankh. 41(7):321-33.

KREITER, E. A.

1927. Contribution to the biology of the barley fly. Rep. Bur. Appl. Ent. 3(1):92-98. (Abst. in R. A. E. Ser. A.)

KUWAYAMA, S., et al.

1955. Investigations on *Hydrellia griseola* Fallen, the smaller rice leaf-miner. Spec. Rep. No. 3. Soc. Plant Prot. North Japan, vii + 180 pp.

LANGE, W. H., JR., K. H. INGEBRETSEN, and L. D. DAVIS

1953. Rice leaf miner: Severe attack controlled by water management, insecticide application. California Agr. 7(8):8-9.

LILLJEBORG, W.

1861. En flugas härjningar å kornfälten i östra skåne, blekinge och södra delarna af kalmar län under sommaren 1860. Tidskr. for landtmanna-och kommunalekonomien, Upsala, pp. 205-15.

LINNANIEMI, W. M.

1913. Zur Kenntnis der Blattminierer, speziell derjenigen Finnlands I. Acta Soc. pro fauna et flora Fennica 37(4):1-138.

LOEW, H.

1860. Neue Beiträge zur Kenntniss der Dipteren. Berlin 7:1-46.

1862. Monographs of the Diptera of North America. Part I. Smithsn. Inst. pp. 129-72.

MACQUART, M.

1835. Histoire naturelle des insectes, Diptères. Tome deuxième. Pourrat Frères, Paris. 703 pp.

MALLOCH, J. R.

1915. Some additional records of Chironomidae for Illinois and notes on other Illinois Diptera. Illinois State Lab. Nat. Hist. Bul. 11:305-64.

MEIGEN, J. W.

1830. Systematische Beschreibung der bekannten europäischen Zweiflugigen Insecten. Teil 6. Hamm, iv + 401 pp.

MUESEBECK, C. F. W.

1933. Seven new species of reared Braconidae (Hymenoptera). Washington Ent. Soc. Proc. 35(9):193-200.

1950. Two new genera and three new species of Braconidae (Hymenoptera). Wash. Ent. Soc. Proc. 52(2):77-81.

NEPVEU, P., and J. D'AGUILAR

1951. Un nouveau ravageur du riz in Camargue. Acad. d'Agr. de France-Procès, Séance du 4 Juil, pp. 463-65.

O'BRIEN, F. E. M.

1948. The control of humidity by saturated salt solutions. Jour. Sci. Instru. 25:73-76.

OETTINGEN, H. VON

1935. Die wichtigsten grasbewohnenden Fliegenlarven Norddeutschlands. Nachr. über Schädlingsbekämpfung 10(2):62-70.

PARKER, H. L., P. A. BERRY, and A. SILVEIRA GUIDO

1951-52. Host-parasite and parasite-host lists of insects reared in the South American parasite laboratory during the period 1940-1946. Rev. Assoc. Ing. Agron. 92:15-112.

PENNAK, R. W.

1953. Fresh-water invertebrates of the United States. Ronald Press Co., New York, ix + 769 pp.

RISBEC, J.

1952. Les insectes nuisibles au riz dans le midi de la France. Riziculteurs de France. Bul. 18, Étude technique 51, pp. 14-19.

ROBINEAU-DESVOIDY, J. B.

1830. Essai sur les myodaires. Mémoires présentés par divers savans A L'Acad. Roy. des Sci. de L'Inst. de France 2(2):813 pp.

RUSCHKA, F., and A. THIENEMANN

1913. Zur Kenntnis der Wasser-Hymenopteren. Ztschr. f. Wiss. Insektenbiol. 9:82-87.

SCHØYEN, T. H.

1930. Beretning om skadeinsektenes optreden i land-og havebruket i årene 1928 og 1929. Landbruksdirekt. Årsberet pp. c1-c36. (Abst. in R. A. E. Ser. A.)

SÉGUY, E.

1934. Faune de France, 28. Diptères (Brachycères). Lechevalier, Paris, 832 pp.

1950. La biologie des Diptères. Encyclopédie Entomologique, serie A, 26. Lechevalier, Paris, 609 pp.

STEIN, J. P. E.

1867. Eine der Gerste schädliche Fliege. Berlin Ent. Ztschr. 11:395-97.

STORMER, K., and R. KLEINE

1911. Die Getreidefliegen, mit besonder Berücksichtigung ihrer wirtschaftlichen Bedeutung und der Abhängigkeit ihres Auftretens von Witterungsverhältnissen. Fühling's Landw. Ztg. 60:682-703.

ULMER, G.

1928. Unsere Wasserinsekten. Quelle and Mener, 2 ed., Leipzig, 157 pp.

VELICKERICH, A. I.

1927. Insects injurious to onions in the Novgorod government. Defense of plants 4(4/5): 717-28. (Abst. in R. A. E. Ser. A.)

WEBSTER, F. M., and T. H. PARKS

1913. The serpentine leaf-miner. Jour. Agr. Res. 1:59-87.

WILKE, S.

1924. Die graue gerstenminier Fliege, *Hydrellia griseola* Fall. (Diptera: Ephydridae). Deut. Ent. Ztschr. 6:172-79.

WILLCOCKS, F. C.

1925. The insect and related pests of Egypt. Part 2. Cairo Sultanie Agr. Soc., Tech. Sec., viii + 418 pp.

ZANGHERI, S.

1956. Un dittero minatore del riso nel basso Ferrarese (*Hydrellia griseola* Fallen, Dipt. Ephydridae). Bollettino Della Soc. Ent. Ital. 86(1-2):12-16.